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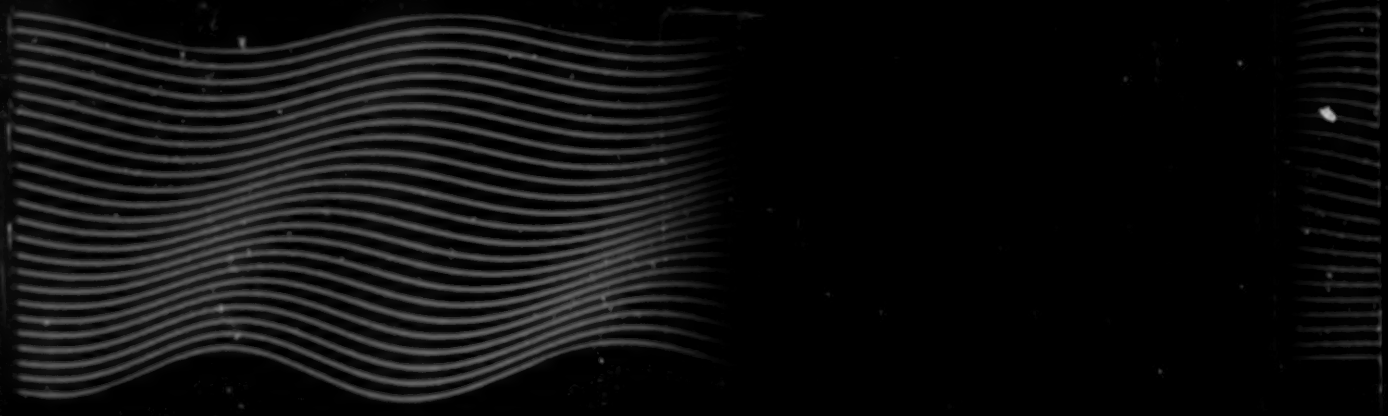

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The effect of selenium on mercury assimilation by freshwater organisms

Nelson Belzile, Yu-Wei Chen, John M. Gunn, Jian Tong, Yves Alarie, Tania Delonchamp, and Chun-Yan Lang

Abstract: In this study, we showed that selenium (Se) deposition from metal smelters in Sudbury, Ontario, greatly reduces the bioassimilation of mercury (Hg) by aquatic biota throughout the food web. Concentrations of total and methyl mercury in tissues of zooplankton, mayflies (*Stenonema femoratum*), amphipods (*Hyalella azteca*), and young-of-the-year perch (*Perca flavescens*) were positively correlated with increasing distance from Sudbury smelters and inversely correlated with Se concentrations in lake water. Although concentrations of total Hg and total Se in tissues showed weak or no correlation in most of the studied aquatic species, methyl mercury and total Se showed much clearer inverse trends. Similar to the results of our previous study of muscle tissue from adult perch and walleye (*Sander vitreus*), these findings suggest that Se plays an important role in limiting the whole-body assimilation of Hg at lower levels of the aquatic food chain. High Se concentrations may force a preferential assimilation of the element over Hg through a competitive adsorption on binding sites. They may also restrict the solubility and availability of Hg to aquatic organisms or reduce the methylation of this metal in lakes.

Résumé : Nous montrons dans cette étude que la déposition de sélénium (Se) provenant des hauts fourneaux de Sudbury en Ontario réduit grandement l'assimilation du mercure (Hg) par le biote aquatique tout au long de la chaîne alimentaire. Les concentrations en Hg total et méthylmercure dans les tissus de zooplancton, éphémères (*Stenonema femoratum*), amphipodes (*Hyalella azteca*) et jeunes perchaudes (*Perca flavescens*) de l'année ont pu être directement corrélées avec la distance qui les sépare des hauts fourneaux de Sudbury et inversement corrélées avec les concentrations de Se dans l'eau de lac. Alors que les concentrations en Hg total et Se total dans les tissus ne montrent que des corrélations faibles ou nulles entre elles chez la plupart des organismes étudiés, le méthylmercure et le Se total montrent des relations inverses beaucoup plus claires. De façon similaire aux résultats de notre étude précédente sur les tissus musculaires de perchaudes et de dorés (*Sander vitreus*) adultes, ces données laissent croire que le Se joue un rôle important en limitant l'assimilation intégrale du Hg aux niveaux inférieurs de la chaîne alimentaire aquatique. Les fortes concentrations de Se pourraient conduire à une assimilation préférentielle de cet élément sur celle du Hg à travers une adsorption compétitive sur des sites de liaison. Elles pourraient aussi restreindre la solubilité et la disponibilité du mercure chez les organismes aquatiques ou réduire la méthylation de ce métal dans les lacs.

Introduction

There is an abundant literature describing interactions between selenium (Se) and mercury (Hg) in living organisms. A report by Parízek and Ošťádalová (1967) was one of the first to identify the protective effect of Se on laboratory rats from kidney intoxication by Hg. Since then, many studies have reported interactions or relationships between Se and Hg in various types of organisms in the laboratory using terrestrial (e.g., Gailer et al. 2000) or aquatic species (e.g., Bjerregaard and Christensen 1993) or even cells or bacteria (e.g., Frisk et al. 2003) and in the field (e.g., Dietz et al. 2000; Chen et al. 2001). A literature review by Cuvin-Aralar and Furness (1991) presented several possible mechanisms of protection, including a redistribution or excretion of Hg in the presence of Se, a competition for binding sites between

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both elements, the formation of Hg–Se complexes, the conversion of toxic forms to less toxic forms of Hg, and the prevention of oxidative damage from Hg by Se through an increased activity of glutathione peroxidase. Among those mechanisms, the formation of an inorganic and (or) protein Hg–Se complex is proposed and frequently supported by analytical evidences derived by traditional chromatographic techniques (Burk et al. 1974; Iwata et al. 1981; Ping et al. 1986), high-performance liquid chromatography (HPLC) combined with inductively coupled plasma-mass spectrometry (ICP-MS; Yoneda and Suzuki 1997*a*, 1997*b*; Sasakura and Suzuki 1998), microscopy (Christensen et al. 1989), or X-ray techniques (Carmichael and Fowler 1980; Lindh and Johansson 1987; Gailer et al. 2000). These complexes are generally found in storage organs such as liver and kidney and even in hair for humans (Soares de Campos et al. 2002). Under high Hg concentrations, a 1:1 molar ratio of Se:Hg is found in tissues (liver) of marine mammals (Koeman et al. 1973, 1975; Dietz et al. 2000), and it has been suggested that methyl mercury (MeHg) could be detoxified by a chemical mechanism involving Se through the formation of metallothioneins and insoluble tienmannite, HgSe (Palmisano et al. 1995; Chen et al. 2002; Ikemoto et al. 2004). However, it seems that the detoxification mechanism could only take place when threshold values of Hg or Se exposure are exceeded in humans (Hansen 1988), other mammals (Hansen et al. 1981; Palmisano et al. 1995; Hoekstra et al. 2003), or birds (Kim et al. 1996). Palmisano et al. (1995) found that co-accumulation of Se and Hg could only occur in dolphin liver above a Hg level of 100 $\mu g \cdot g^{-1}$ wet weight. Similarly, it was suggested that the storage of a Hg–Se complex can only take place at higher molar ratios of Se:Hg (Hansen 1988).

Some recent studies have also tried to relate the inhibitory effects of Se on Hg toxicity to specific enzymatic activities (El-Demerdash 2001; Farina et al. 2003). A significant decrease was observed in the protein content of brain and liver of rats and in several enzymes in brain, liver, plasma, and serum in response to Hg treatment. The action of Se was positive in alleviating the toxic effects of Hg on different enzymes (El-Demerdash 2001). The formation of an inactive ternary complex of the thiol-Hg-Se type to prevent the inhibition of δ-aminolevulinate dehydratase was proposed by Farina et al. (2003).

In freshwater environments, the bioaccumulation of Hg by biota was retarded by elevated concentrations of Se in water of experimental ecosystems (Rudd et al. 1980; Turner and Rudd 1983; Turner and Swick 1983) and Se-treated lakes (Paulsson and Lundberg 1989). Similarly, Hg concentrations in largemouth bass (*Micropterus salmoides*) increased significantly after the elimination of Se-rich discharges to a quarry pond (Southworth et al. 1994, 2000). In a previous study (Chen et al. 2001), we reported significant inverse relationships between total concentrations of Hg and Se in muscle tissues from yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*) from the Sudbury area. There are, however, very few studies on Se–Hg antagonistic effects done on biological species at the lower level of the aquatic food chain partly because of the analytical challenges in working with small sample sizes and trace elements. Other researchers have reported that the protective action of Se against Hg toxicity is not obvious in invertebrates (Pelletier 1986; Patel et al. 1988; Wang et al. 2004).

In this study, we complete our investigation on Se–Hg interactions in the aquatic food web with organisms positioned at lower levels of the food chain in Sudbury lakes near the large source of Se emissions. We use the results to suggest possible mechanisms for the observed inverse relationships between concentrations of MeHg and Se in tissues.

Materials and methods

Sampling and sample preparation

Test organisms consisted of three primary consumers (pelagic crustacean zooplankton, the mayfly *Stenonema femoratum* (Ephemeroptera), and the amphipod *Hyalella azteca* (Crustacea, Amphipoda)) and two secondary consumers (the water beetle *Graphoderus liberus* (Coleoptera) and young-of-the-year (YOY) *Perca flavescens* collected in lakes that are situated 5–65 km from the Sudbury metal smelters. The study lakes exhibit a moderate range of limnological and chemical characteristics and were selected to avoid high confounding gradients in chemical variable such as dissolved organic carbon or pH that could affect Hg assimilation (Table 1).

Mayflies were hand picked from shallow rocky shorelines. Amphipods were collected with dip nets and sorted under a dissecting scope. Zooplankton specimens were collected at mid-lake using small Wisconsin nets and then passed through sieves to retain the fraction between 250 and 1000 µm. Zooplankton samples were not sorted to species but rather represent composites of the size and species encountered in the pelagic zone of these boreal shield lakes. YOY perch were collected in littoral zones using seine nets. All perch were <40 days old. Larvae of *Graphoderus liberus* (Coleoptera) were collected at three different growth stages from only one lake (Swan Lake) to study Se and Hg assimilation. In this lake, a total of 1092, 100, and 204 individuals of *G. liberus* were hand picked at each consecutive growth stage. Organisms were collected between the end of May and the beginning of July 2002, carefully rinsed in double distilled water, and kept frozen until digestion and analysis. Mayflies and amphipods were depurated for 24 h in fresh water before being frozen. Samples were then freeze-dried, ground, and kept ready for digestion and analysis.

Analyses

For the determination of total Hg and total Se in tissues, a microwave digestion was performed in a mixture of HNO_3 and H_2O_2. Total Se and Hg were determined by hydride generation atomic fluorescence spectrometry (model PSA 10.055 Millenium Excalibur; PS Analytical, Orpington, Kent, UK) and by cold vapour atomic fluorescence spectrometry (model Tekran Mercury Analyzer 2600; Tekran Inc., Toronto, Ontario), respectively. The determination of MeHg in tissues was preformed according to the method developed by Liang et al. (1996) with slight modifications. Briefly, dry samples were digested with 2.0 mL of 25% (*w*/*v*) KOH–methanol solution in a Teflon vial at 85 °C for 3 h. The back extraction was performed on acidified digests with 6.0 mL.

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Table 1. Limnological and chemical characteristics of the studied lakes.

Lake	Latitude (°N)	Longitude (°W)	Distance from smelters (km)	Surface area (ha)	Mean depth (m)	pH	DOC ($mg \cdot L^{-1}$)	Ca ($mmol \cdot L^{-1}$)	Mg ($mmol \cdot L^{-1}$)	[Hg] ($pmol \cdot L^{-1}$)	[Se] ($nmol \cdot L^{-1}$)
Long (Lo)	46°22′	81°05′	8	792	7.2	7.0	4.1	0.19	0.11	12.6	1.8
Lohi (Li)	46°23′	81°02′	8	41	6.2	6.2	3.4	0.10	0.05	10.9	2.1
Swan (Sw)	46°22′	81°04′	9	5.8	2.8	5.7	2.8	0.08	0.02	10.9	1.9
Bethel (Be)	46°28′	80°57′	10	31	2.7	8.1	7.7	0.32	0.22	6.5	2.1
McFarlane (Mc)	46°25′	80°59′	11	166	7.3	7.4	4.6	0.35	0.19	10.2	2.5
Ramsey (Ra)	46°28′	80°57′	12	795	9.2	7.4	3.5	0.33	0.18	12.3	2.9
Nelson (Ne)	46°43′	81°05′	28	309	11.1	6.6	2.0	0.06	0.03	9.3	1.5
Windy (Wi)	46°35′	81°26′	32	1129	10.7	6.5	2.8	0.08	0.05	16.5	1.4
Geneva (Ga)	46°45′	81°33′	50	356	6.3	6.8	4.2	0.10	0.02	13.5	0.8
George (Ge)	46°01′	81°24′	52	189	16.4	6.3	2.2	0.04	0.02	10.4	0.9
Halfway (Ha)	46°53′	81° 38′	65	247	8.0	6.9	4.4	0.11	0.06	16.0	0.5

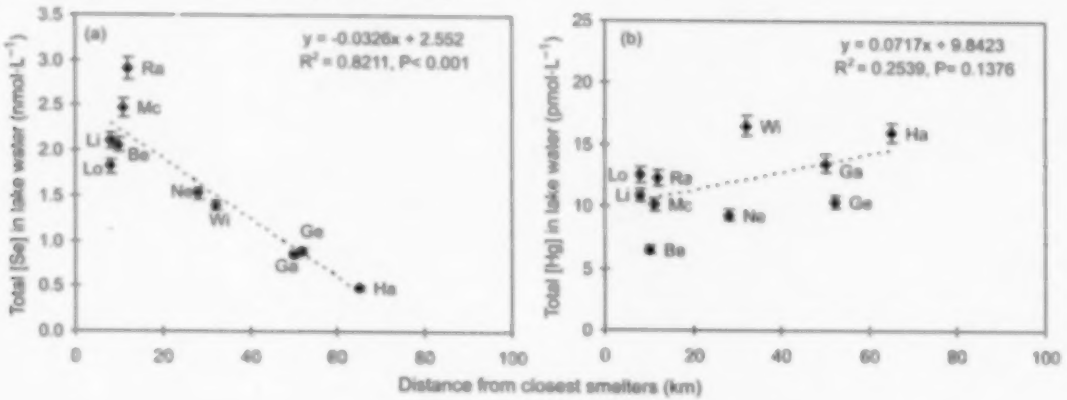
Note: DOC, dissolved organic carbon.

Table 2. Quality of analytical results.

	Total Se			Total Hg			MeHg		
CRM	Certified value	Our results	Relative error (%)	Certified value	Our results	Relative error (%)	Certified value	Our results	Relative error (%)
DORM-2 ($\mu g \cdot g^{-1}$)	1.40±0.09	1.38±0.10	1.4	4.64±0.26	4.59±0.34	1.1	4.47±0.32	4.31±0.34	3.6
TORT-2 ($\mu g \cdot g^{-1}$)	5.63±0.67	5.59±0.46	0.7	0.27±0.06	0.29±0.05	7.4	0.152±0.013	0.142±0.017	6.6
ORMS-2 ($ng \cdot L^{-1}$)	—	—	—	30.6±2.3	32.2±2.1	5.2	—	—	—

Note: DORM-2, TORT-2, and ORMS-2 are certified reference materials (CRM) from the National Research Council of Canada.

Fig. 1. Concentrations of total dissolved selenium (Se) (*a*) and mercury (Hg) (*b*) as a function of distance of sampled lakes from the closest Sudbury smelters. Lake abbreviations are as follows: Long, Lo; Lohi, Li; Swan, Sw; Bethel, Be; McFarlane, Mc; Ramsey, Ra; Nelson, Ne; Windy, Wi; Geneva, Ga; George, Ge; Halfway, Ha.


(a)
y = -0.0326x + 2.552
R² = 0.8211, P< 0.001
Total [Se] in lake water (nmol·L⁻¹)
(b)
y = 0.0717x + 9.8423
R² = 0.2539, P= 0.1376
Total [Hg] in lake water (pmol·L⁻¹)
Distance from closest smelters (km)

of CH_2Cl_2. The extracted MeHg in CH_2Cl_2 was collected and the ethylation step followed. MeHg (in the form of methyl ethyl mercury after ethylation) collected on the Tenax tube was analyzed by gas chromatography – cold-vapor atomic fluorescence spectrometry. The analytical quality was controlled by using the certified reference materials (CRM) DORM-2 and TORT-2 from the National Research Council of Canada at a frequency of one CRM control, a triplicate digestion, and a standard spike recovery for every 10 digested tissue samples (Table 2). The relative error on total Se and total Hg measurements in tissues was 5%–7%; it was 8%–12% for MeHg. Water samples were collected in acid-cleaned glass bottles opened below the lake surface, with all required precautions to limit contamination according to US Environmental Protection Agency method 1631. Total Se and Hg in lake water were determined by the same analytical techniques previously mentioned (Chen et al. 2001), and the quality of analysis for Hg was controlled by

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Table 3. Concentrations of Se, Hg, and percentage of Hg as MeHg in tissues of aquatic organisms expressed on a dry weight basis.

	Zooplankton			Amphipod (*Hyalella azteca*)			Mayfly (*Stenonema femoratum*)			YOY perch (*Perca flavescens*)		
Lake	Se-total (nmol·g^{-1})	Hg-total (pmol·g^{-1})	MeHg (%)	Se-total (nmol·g^{-1})	Hg-total (pmol·g^{-1})	MeHg (%)	Se-total (nmol·g^{-1})	Hg-total (pmol·g^{-1})	MeHg (%)	Se-total (nmol·g^{-1})	Hg-total (pmol·g^{-1})	MeHg (%)
Long (Lo)	56	145	19	30	41	41	88	65	15	79.5	403	32
Lohi (Li)	129	184	31	—	—	—	132	130	16	—	—	—
Bethel (Be)	46	85	49	20	47	45	—	—	—	39.1	191	74
McFarlane (Mc)	48	95	36	21	55	40	69	50	19	68.4	294	78
Ramsey (Ra)	63	135	23	35	39	56	99	100	18	96.8	293	61
Nelson (Ne)	86	150	30	76	135	13	155	145	17	135.2	340	56
Windy (Wi)	80	281	27	17	116	47	90	105	48	76.7	543	79
Geneva (Ga)	29	284	30	26	141	30	71	198	25	41.8	543	71
George (Ge)	70	364	37	—	—	—	102	239	17	—	—	—
Halfway (Ha)	22	398	54	12	174	54	56	419	16	34.5	1221	41
Average			34			41			22			62

Note: Average concentrations of Se, Hg, and percentage of Hg as MeHg in *Gryphaeleras libera* collected in Swan Lake only were 94 nmol·g^{-1}, 164 pmol·g^{-1} (dry weight), and 48%, respectively. Relative errors on all Se and Hg determinations were at 5%–7% and at 8%–12% for MeHg. YOY, young-of-the-year.

using the certified standard ORMS-2 from the National Research Council of Canada (Table 2). MeHg was not determined in lake waters.

Statistical treatment

Relationships between variables were examined using bivariate scatterplots. When a possible linear relationship was indicated, a simple regression model was tested using Microsoft Excel (Microsoft Corporation, Redmond, Washington). When bivariate plots appeared to be nonlinear, nonlinear regression models with least-squares were tested using the same program. Test of difference between slopes was done using the analysis of covariance (ANCOVA) and comparison between taxonomic groups and primary and secondary consumers using the analysis of variance (ANOVA).

Results and discussion

The effect of distance from smelters

Concentrations of total Se in lake water varied from 2.91 to 0.48 nmol·L^{-1}, showing the clear effect of declining concentration with distance from the nearest smelters (Table 1). However, the concentrations of total Hg in lake water remained very low with distance from the smelters (Table 1; see also the poor regression of Fig. 1*b*). The presence of higher Se levels in lakes close to Sudbury is directly related to mining and smelting activities, and several tons of Se are released annually to the environment through atmospheric emissions (Nriagu and Wong 1983). To confirm the source of these elements, four ore samples coming from different mines of Inco Limited were analyzed for their total contents in Se and Hg using the above analytical methods. Total Se levels were more than 1000 times higher (62 ± 18 μg Se·g^{-1}) than levels of total Hg (58 ± 22 ng Hg·g^{-1}) in these ores. Differences in emission levels could therefore explain the different trends between total Se and total Hg in surface waters as function of distance from smelters (Fig. 1). The low level of Hg in the ore and the ubiquitous nature of Hg in the environment due to its long-range transport from a variety of other sources may in turn explain the lack of a distance effect on Hg in lake water near Sudbury.

When total Hg and MeHg concentrations (expressed on a dry weight basis; Table 3) were plotted against the distance from smelters, significant, positive linear relationships were obtained in all four studied species or taxonomic groups (Fig. 2). The difference in the two slopes (all p values <0.05 as tested by ANCOVA) suggests that the percentage of MeHg decreased in studied organisms with increasing distance from the Se source. The average percentage of MeHg in tissues increased from mayfly (22%) to zooplankton (34%), amphipod (41%), water beetle (48%), and larval perch (62%). These results could suggest a biomagnification of MeHg along the food chain. It has been shown that MeHg in muscle tissue of adult fish generally exceeds 85% of the total Hg (e.g., Bloom 1992).

In lakes that were affected more directly by Se deposition, the concentration of MeHg in tissues was significantly different between taxonomic groups (ANOVA, $p < 0.001$): mayfly and amphipod were significantly lower and larval perch were significantly higher than all others, but zooplankton and *G. liberus* were intermediate (Tukey's post hoc test).

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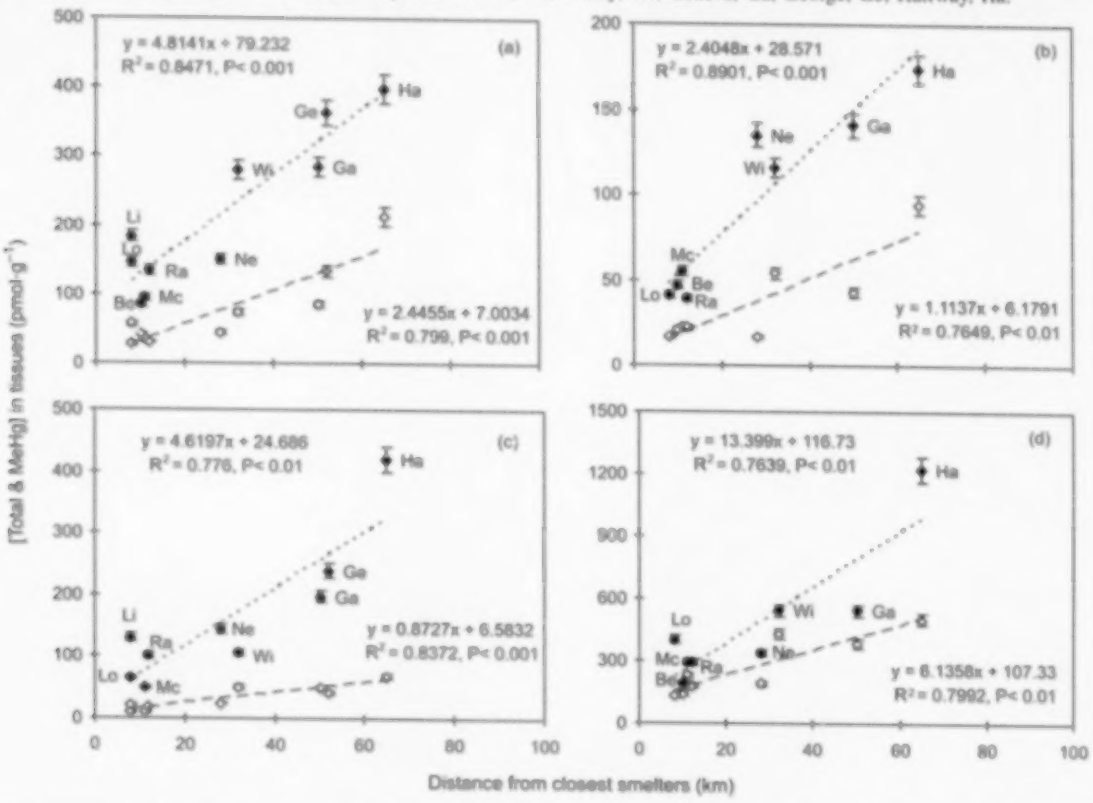

Fig. 2. Concentrations of total mercury (Hg) (solid symbols) and methyl mercury (MeHg) (open symbols) in tissues (dry weight) of zooplankton (*a*), amphipods (*Hyalella azteca*) (*b*), mayflies (*Stenonema femoratum*) (*c*), and young-of-the year perch (*Perca flavescens*) (*d*) as a function of distance of sampled lakes from the closest Sudbury smelters. Lake abbreviations are as follows: Long, Lo; Lohi, Li; Swan, Sw; Bethel, Be; McFarlane, Mc; Ramsey, Ra; Nelson, Ne; Windy, Wi; Geneva, Ga; George, Ge; Halfway, Ha.

When the taxonomic groups were pooled into primary consumers (zooplankton, mayfly, and amphipod) or secondary consumers (*G. liberus* and YOY perch), the former had significantly lower MeHg than the latter (ANOVA, $p < 0.001$). The percentages of MeHg reported here are consistent with values reported in the literature for similar organisms (e.g., Bloom 1992; Gorski et al. 2003). However, the absolute concentrations of total Hg and MeHg in zooplankton and invertebrates were much lower in the Sudbury area than those reported by Gorski et al. (2003) in inlands lakes of Isle Royale National Park in Lake Superior (e.g., 1000 pmol total Hg·g^{-1} dry wt for bulk zooplankton compared with 130 ± 40 pmol Hg·g^{-1} in Sudbury lakes) or in insect larvae from Quebec hydroelectric reservoirs, with average concentrations up to 10 times the levels in larvae from natural lakes (Tremblay and Lucotte 1997).

In our study, the protective effect of Se is demonstrated by the significant inverse linear regression between concentrations of MeHg in tissues and levels of total dissolved Se in lakes for all species (Fig. 3). These results suggest that Se affects the concentrations of MeHg in the studied species.

Se versus Hg and MeHg in tissues

In a previous study, we reported highly significant correlations (R^2 = 0.79–0.97) between concentrations of total Hg and total Se in adult perch and walleye muscle tissue (Chen et al. 2001). In the present study with zooplankton, mayfly, amphipod, and yearling perch, no statistically significant relationships between tissue total Hg and total Se in the whole body measurements of the four taxa were detected. Slightly stronger inverse trends were observed for MeHg (Figs. 4*b*, 4*d*, 4*f*, and 4*h*), although the relationships were not statistically significant at $p < 0.05$.

Less clear Se–Hg relations were expected when using species positioned at low levels of the food chain, especially with species such as zooplankton, which have a much shorter life-span than fish. In these taxa, the variations in bioassimilation because of lake-to-lake differences in physico-chemical characteristics such as the size of the basin, temperature, nutrients, food structure, etc. are expected to be much greater than in long-lived fish. Better correlations are obtained when using MeHg instead of total Hg presumably because MeHg concentrations more closely reflect biological assimilation, whereas total Hg concentration can reflect contribution from nonbioavailable forms: those present in incompletely depurated guts or in shells. These findings suggest that MeHg rather than total Hg is a better indicator for studies of assimilation, particularly when the concentration of Hg in a biological sample is extremely low. It should be noted that the correlation between MeHg and

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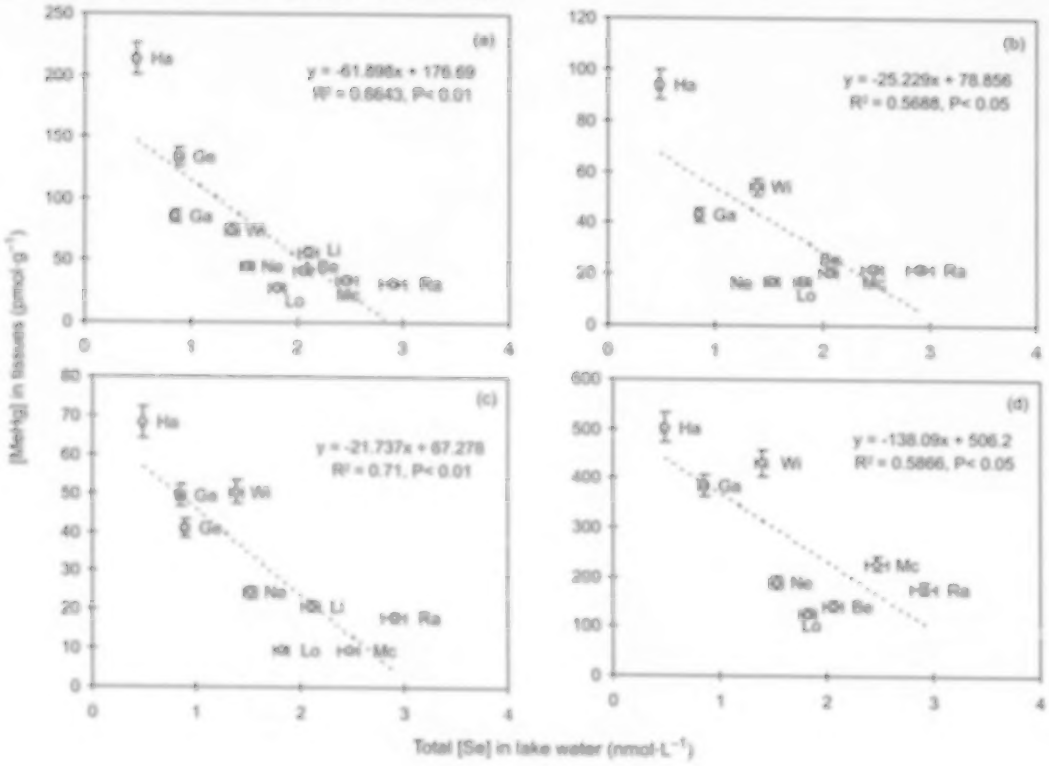
Fig. 3. Concentrations of methyl mercury (MeHg) in tissues (dry weight) of zooplankton (*a*), amphipods (*Hyalella azteca*) (*b*), mayflies (*Stenonema femoratum*) (*c*), and young-of-the-year perch (*Perca flavescens*) (*d*) as a function of concentrations of total dissolved selenium (Se) in lake water. Lake abbreviations are as follows: Long, Lo; Lohi, Li; Swan, Sw; Bethel, Be; McFarlane, Mc; Ramsey, Ra; Nelson, Ne; Windy, Wi; Geneva, Ga; George, Ge; Halfway, Ha.



total Se in mayfly is poorer than that in other species. This is perhaps due to the particular nature of this species. Mayflies have relatively large amounts of hard exoskeletons that caused greater difficulties during steps of sample grinding, digestion, and MeHg extraction. The percentage of MeHg in mayfly was also the lowest (Fig. 2), consistent with a study of the mayfly *Hexagenia* sp. (Gorski et al. 2003). Se concentrations in organisms did not appear to be related to Se concentrations in lake water. This finding may be due to the fact that trace element bioaccumulation in organisms is a complex process that includes uptake of food, suspended particles, and sediment contact.

Significant inverse relationships between total Hg and MeHg and total Se were found when comparing the three larval stages of the water beetle *G. liberus* in Swan Lake (Fig. 5). Surprisingly, the concentrations of total Hg and MeHg were lower at growth stage 2 than at stages 1 and 3, while the concentration of total Se was the highest at this intermediate stage. A slightly lower proportion of MeHg was also observed (41% compared with 49% at stages 1 and 3, respectively). The results indicate that for some reason, larvae preferentially assimilated larger amounts of Se at their second growth stage, which in turn caused a lower level of MeHg and total Hg in their body. It could also be due to an unmeasured change in water quality or feeding habits during the three-stage period.

Possible mechanisms of interaction

Se and MeHg molar ratios within tissues and between tissue and water concentrations were calculated for all samples. Ranges of ratios and average values for the lakes close (<15 km) to Sudbury smelters are presented (Table 4). Ratios comparing concentrations in organisms and in water (columns 3 and 4) were calculated based on molar concentrations in wet tissue; that is, Se or MeHg concentrations in dry samples converted to those in wet tissues according to their respective water contents: 80%–85% for yearling perch, 84%–88% for amphipod and mayfly, 75%–87% for *G. liberus*, and 95%–98% for zooplankton. Ratios of Se-organism/Se-water (3rd column) and those of MeHg-organism/Hg-water (4th column) indicate a strong enrichment factor or bioconcentration of both elements in tissues compared with water, with Se ratios being much larger than Hg ratios. Higher Se-organism/Se-water ratios suggest a preferential assimilation of Se compared with total Hg in all organisms. This is expected because Se is an essential element, while Hg is not. A preferential affinity of binding sites for Se could exist and that could explain how Se plays an antagonistic role on the assimilation of MeHg in aquatic organisms. Even in lakes near the smelters where Se concentrations are high, ratios of MeHg-organism/Hg-water demonstrated the continued biomagnification of Hg in the food chain. The enrichment factors for the primary consumers

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Fig. 4. Concentrations of total mercury (Hg) (left panels) and methyl mercury (MeHg) (right panels) in tissues (dry weight) of zooplankton (*a*, *b*), amphipods (*Hyalella azteca*) (*c*, *d*), mayflies (*Stenonema femoratum*) (*e*, *f*), and young-of-the-year perch (*Perca flavescens*) (*g*, *h*) as a function of concentrations of total selenium (Se) in tissues of the same organism. Lake abbreviations are as follows: Long, Lo; Lohi, Li; Swan, Sw; Bethel, Be; McFarlane, Mc; Ramsey, Ra; Nelson, Ne; Windy, Wi; Geneva, Ga; George, Ge; Halfway, Ha.

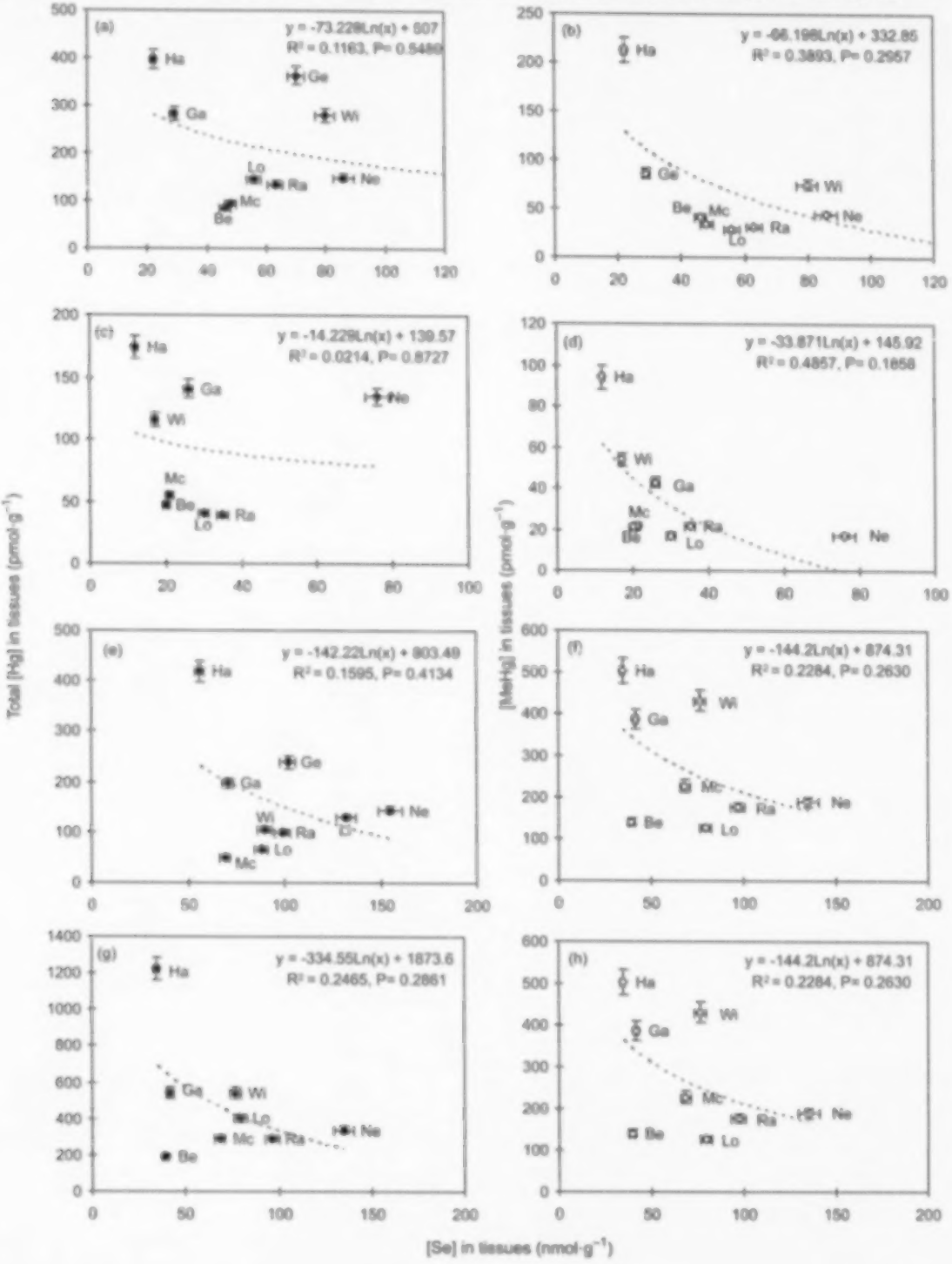

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Table 4. Comparison of calculated molar ratios.

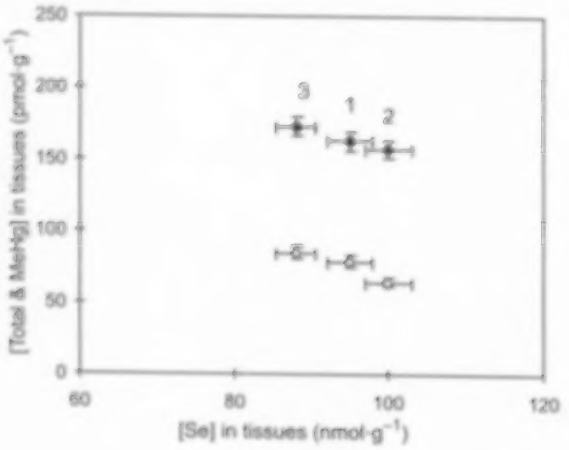
Medium	Se/MeHg	Se-organism/Se-water[a]	MeHg-organism/Hg-water[a]
Zooplankton	103–2263 (1760±485)	650–2360 (930±520)	70–400 (120±55)
Mayflies (*Hyalella azteca*)	820–9263 (7085±1620)	1020–3500 (1300±465)	100–550 (160±68)
Amphipods (*Stenonema femoratum*)	128–4471 (1316±425)	1100–6460 (1520±460)	170–760 (280±105)
YOY perch (*Perca flavescens*)	69–714 (437±175)	4150–13260 (4640±1550)	1510–4720 (2580±890)
Graphoderus liberus	(1260±250)	(8060±1410)	(1140±345)
Adult perch (*Perca flavescens*)[b]	(820±210)	(14380±2650)	(7200±1450)
Adult walleye (*Sander vitreus*)[b]	(104±44)	(5900±1460)	(11200±3620)

Note: Data are shown as a range of values for all studied lakes. All values in parentheses represent an average (±SD) for lakes that are located within 15 km of Sudbury smelters. YOY, young-of-the-year.

[a]Expressed on a wet weight basis.

[b]Estimated average ratio of Se-organism over MeHg and that of MeHg-organism over total Hg in water, assuming that 95% of measured Hg in fish muscles is MeHg.

Fig. 5. Concentrations of total mercury (Hg) (closed symbols) and methyl mercury (MeHg) (open symbols) in tissues (dry weight) of the three larval stages of *Graphoderus liberus* as a function of concentrations of total selenium (Se) in tissues of the same organism.



were at 120 for zooplankton, 160 for mayfly, and 280 for amphipods. Secondary consumers showed much larger ratios, with average values of 1140 for *G. liberus* and 2580 for YOY perch. For comparison with higher levels of the food chain, adult perch were estimated at 7200, while the top predator walleye was at 11 200, using data from Chen et al. (2001). The pattern for Se was the same, but the biomagnification of Se seemed to stop at the level of yellow perch (14 380) and actually declined at the level of walleye (5900) (Table 4). This could be due to mass dilution in larger fish. The molar ratio of Se-organism to MeHg-organism also indicates that the proportion of Se in tissues compared with that of MeHg decreased when moving upward in the food chain. It might again indicate a preferential assimilation of Se by primary consumers. This is especially noticeable in mayfly, where high ratios could reflect the feeding mechanisms of the species. *Stenonema femoratum* grazes the organic film of submerged surfaces where benthic algae and sediment particles rich in Se can be found in Sudbury lakes.

It has also been suggested that Se could reduce the methylation rate of Hg (Jackson 1991; Jin et al. 1997, 1999) and the bioaccumulation of MeHg in species living in sediments by limiting the solubility of Hg (Nuutinen and Kukkonen 1998). Se levels are indeed very high in Sudbury lake sediments and can reach several micrograms per gram (ppm) (Nriagu and Wong 1983; Belzile et al. 2000). Such high Se levels could limit the solubility and consequently the methylation of Hg as well as its bioavailability. Several earlier studies (see Introduction) also speculated that threshold values of Hg or Se must be reached before antagonistic effects or detoxification mechanisms through the formation of HgSe compounds could occur. That could further explain why the antagonistic phenomenon is more clearly observed close to Sudbury, where Se levels in lakes and sediments are very high. Additional data on Hg and Se concentrations in fish organs such as liver will help to confirm or refute this last hypothesis.

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Elucidating patterns of size-dependent predation on larval yellow perch (*Perca flavescens*) in Lake Michigan: an experimental and modeling approach

Richard S. Fulford, James A. Rice, Thomas J. Miller, and Fred P. Binkowski

Abstract: Yellow perch (*Perca flavescens*) in Lake Michigan have experienced sustained recruitment failure since 1990 as a result of increased mortality during the pelagic larval phase. Increased mortality of larval yellow perch has been tied indirectly to increased alewife (*Alosa pseudoharengus*) predation, but effects of predation on larval survival variability must be better understood. We compared the relative importance of predation by alewife and two other fish predators to larval survival in laboratory experiments and developed an individual-based predation model (IBM) to examine patterns in size-dependent predation vulnerability. Simulations exposing larval perch to predation by all predators suggest that larval mortality resulting from alewife predation is more size-dependent than mortality resulting from the other two predators, and the range of sizes vulnerable to alewife is smaller. Alewife predation may not be an important mortality source for larval yellow perch in Lake Michigan at present because of the narrow range of vulnerable sizes and low densities of larval perch in the open lake. Predation is more likely to be important in smaller, more productive systems where other predators are abundant. Modeling results also indicate IBM analysis of date of hatch distributions of surviving larvae is a valuable tool for identifying factors most important to larval survival.

Résumé : Les perchaudes (*Perca flavescens*) du lac Michigan subissent un échec soutenu de leur recrutement depuis 1990 à cause d'une augmentation de la mortalité durant leur phase larvaire pélagique. La mortalité accrue des larves de perchaude a été reliée à l'augmentation de la prédation par le gaspareau (*Alosa pseudoharengus*), mais les effets de la prédation sur la variabilité de la survie larvaire doivent être mieux compris. Nous avons comparé l'importance relative de la prédation par le gaspareau et par deux autres poissons prédateurs sur la survie larvaire dans des expériences de laboratoire et nous avons mis au point un modèle de prédation basé sur l'individu (IBM) pour examiner les patrons de vulnérabilité à la prédation en fonction de la taille. Des simulations qui exposent des larves de perchaude à l'ensemble des prédateurs laissent croire que la mortalité larvaire due au gaspareau est plus fonction de la taille que celle due aux deux autres prédateurs et que la gamme des tailles vulnérables au gaspareau est plus étroite. La prédation par le gaspareau peut ne pas être actuellement une cause importante de mortalité chez les larves de perchaude au lac Michigan à cause de la marge réduite des tailles vulnérables et à cause des faibles densités de larves de perchaude dans les eaux du large. La prédation est vraisemblablement plus importante dans les systèmes plus petits et plus productifs où il y a abondance d'autres prédateurs. Les résultats de la modélisation montrent que l'analyse IBM de la date d'éclosion des larves survivantes est un outil précieux pour identifier les facteurs qui sont les plus importants pour la survie des larves.

[Traduit par la Rédaction]

Introduction

Annual recruitment variability in fishes is often significantly affected by survival during the larval phase. Cumulative larval mortality can be 99% or more, and relatively minor changes in this value can translate to large differences in the size of an annual cohort (Houde 1987, 1989; Sissenwine 1984). Mortality during the larval stage is particularly important for yellow perch (*Perca flavescens*) in Lake Michigan. Population levels of yellow perch in Lake Michigan have been highly variable over the last 30 years and have been in decline since 1994 (Francis et al. 1996). The present decline is widely thought to be the result of increased larval mortality (Clapp and Makauskas 2002). Increased vulnerability to size-dependent predation is one primary hypothesis for reduced survival during the larval stage.

One consequence of high larval mortality rates is that traditional approaches to analyzing patterns in survival based

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on the average characteristics of a cohort can be misleading because the "average" larva often does not survive (Sharp 1987). Instead, it may be more informative to ask whether the survivors of the larval phase are a random subgroup of the population or a nonrandom group that possesses some inherent advantage when compared with other members of the cohort. In cases where selective mortality occurs, an analysis of the change in key characteristics of survivors has proven valuable for detecting the causes of selective mortality in larval fishes (e.g., Crecco and Savoy 1985; Rice et al. 1987; Leggett and Deblois 1994).

Larval mortality is typically size-dependent (Miller 1988; Sogard 1997). Analysis of factors affecting size-dependent mortality in larval fishes is difficult because selective forces are hard to detect from field data (Miller 1997), and appropriate factorial experiments are often prohibitive because of time and expense. One approach that has born fruit in the past is the use of individual-based simulation models (IBM). Examination of general patterns in larval survival with IBMs has established several common threads, e.g., the intensity of size-dependent vulnerability to predation in larval fishes varies with changes in larval growth rate (Letcher et al. 1996*a*; Rice et al. 1993) and between predator types (Cowan et al. 1996).

In addition to growth rate variability, an often overlooked and potentially important source of size variability for a larval cohort is variation in individual date of hatch (DOH). Date of hatch often varies by days or weeks, resulting in size differences among larvae because of differences in the amount of time they have had to grow. In fact, timing of hatch may be as important, or more important, than growth rate in the development of size variability within an annual larval cohort. Variation in the timing and intensity of size-selective predation is likely to affect the relationship between larval survival and DOH. Predator density can vary significantly over the larval period, resulting in differences in predation vulnerability over time for individual larvae because of changes in encounter rate with particular predator species (Brandt et al. 1987). It is important to understand how all aspects of size variability contribute to size-dependent predation vulnerability, and comparisons of all potential contributing factors in a modeling framework will be more informative regarding the importance of particular factors than is possible from field data alone.

We conducted a series of laboratory experiments to quantify size-dependent vulnerability of larval yellow perch to three natural predators: alewife (*Alosa pseudoharengus*), white perch (*Morone americana*), and adult yellow perch. Alewife are the most commonly cited predator of larval fishes in Lake Michigan (Crowder 1980; Shroyer and McComish 2000). White perch and adult yellow perch, while not present in the pelagic zone of Lake Michigan, would come into contact with larval perch in smaller lakes and have been observed to consume larval yellow perch if given the opportunity (Fulford 2003). We also examined how these relationships are affected by larval condition, larval density, and the presence of alternative prey. We used these data to build a predator–prey IBM that takes into account variability in both growth rate and DOH, as well as differences in size dependence of predation among predator types. We used this IBM to examine changes in the DOH distribution of survivors resulting from two typical patterns of size-dependent mortality: changes in mortality resulting from changes in larval growth rate and from changes in the timing and intensity of size-selective predation. Changes in the timing and intensity of predation are hypothesized to increase the importance of DOH in determining the predation vulnerability of individual larvae. We ask two broad questions. Is this IBM analysis useful for interpretation of DOH distributions of larval yellow perch survivors? Does predation limit survival of larval yellow perch in Lake Michigan.

Methods

Larval yellow perch used in all of the experiments were hatched in the laboratory from egg skeins stripped and fertilized in the field during May from 1999 to 2001. These skeins were collected from ripe females captured in gill nets during the peak of spawning for yellow perch in Lake Michigan waters near Milwaukee, Wisconsin. Each female produces one skein per year. Up to 10 skeins were collected each season over a 1- to 2-day period, and these were individually fertilized in the field with the milt from 3 to 6 males. Fertilized skeins were returned to the Great Lakes WATER Institute Aquaculture Lab and placed on plastic platforms in a 2.4 m diameter tank with minimal flow and ambient temperature conditions (10–11 °C).

Beginning two days after egg fertilization, temperature was raised 1 °C every other day until hatching was observed. This procedure decreases development time and increases hatching success in the laboratory (Fred Binkowski, unpublished data). Hatching began within 10–14 days, and larvae were maintained in the same tank at 15 °C under flow-through conditions for the duration of the experimental season. Larvae were fed a staged diet over the experimental period beginning with small cultured zooplankton and followed by *Artemia* nauplii, ground-up beef liver, and finally a commercial pellet feed. A staged feeding protocol has been shown to maximize growth and survival for yellow perch larvae in the lab (Fred Binkowski, unpublished data).

Predators used in these experiments were adult alewife, adult white perch, and adult yellow perch. In the fall of the year preceding the experiments, juvenile alewives were captured with beach seines in water less than 1.5 m deep from various sites near Milwaukee, Wisconsin, and were maintained in the laboratory until the following spring. Adult white perch were captured with gillnets in Green Bay, Wisconsin, in the late fall and were maintained in the laboratory until the following spring. Yellow perch were available in the laboratory from previous years' spawning activities (described above). All predators were maintained at 15 °C in flow-through systems and were fed a maintenance ration of commercial, pelleted food until the beginning of the experimental season.

Probability of capture

This experiment was conducted in June–July 1999 and June–July 2001. In 1999, an experimental system was set up consisting of eight 145 L rectangular tanks, each with a glass observation panel on one side. The tanks were isolated visually by surrounding them with a black plastic curtain. Each tank was covered with an opaque plastic lid fitted with

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a polyvinyl chloride (PVC) tube extending from above the tank through the cover into the tank interior. This tube was used to introduce fish larvae without disturbing the predators in the tank.

At the beginning of the acclimation period, each tank received five predators of a single species. White perch (150–193 mm total length, TL) were placed in four tanks and adult yellow perch (144–157 mm TL) were placed in the other four; tanks were randomly assigned to species. Total length of each individual predator was measured to the nearest 1 mm before introduction. These predators were allowed to acclimate to the tank for 7 days before the beginning of a trial. Trial tanks were maintained at a temperature of 17 °C and a mean flow of 3.5 L·min^{-1}. The acclimation period included the introduction of yellow perch larvae as a food source to re-acclimate the predators to live food. During the acclimation period, the fish were not disturbed unless a predator died and had to be removed. Predator mortality typically occurred only in the first 1–2 days after transfer. All feeding was conducted via the feeding tube, and all feeding was halted 24 h before the beginning of an experimental trial.

At the beginning of an experimental trial, 25–50 yellow perch larvae were introduced into an individual test tank. From the moment of introduction, an observer watched all activity in the tank through a small observation hole cut into the black plastic screen. A second participant stood behind the tank to introduce larvae through the PVC tube, keep time, and record all observations. The observer would pick a single predator in the tank and verbally identify successful and unsuccessful strikes for 30 s; these strikes would be recorded by the second participant. At the end of 30 s, the observer would arbitrarily choose another predator and repeat the process. This single-predator observation method was used to minimize overestimation of capture success resulting from observer bias. Each trial lasted 30 min: an additional 25–50 larvae were introduced through the tube if larvae in the tank were more than 75% depleted prior to the 30-min mark. If less than 10 strikes were observed in any 30-min trial, then that trial was not used for analysis. This procedure was then repeated in sequence for the remaining seven experimental tanks. Trials were conducted with larval yellow perch prey at 7 days posthatch (dph) (TL mean ± standard deviation (SD), 7.5 ± 0.43 mm), 15 dph (9.2 ± 0.82 mm), 30 dph (12.8 ± 1.29 mm), and 45 dph (23.0 ± 1.78 mm).

During pretrial observations in 1999, we established that alewife would not acclimate to the rectangular tanks and begin feeding within a reasonable time. For this reason, alewife trials were conducted in 2.4 m diameter round tanks. We also noted that normal feeding activity was observed more often if alewife were kept in larger groups, so alewife trials were conducted with groups of 50–100 alewives per tank (113–180 mm TL), rather than five as with white perch and yellow perch. Alewife trials were conducted June–July 2001 in a manner similar to that described for other predator species, with the exception that a larger number of yellow perch larvae was introduced into each tank to maintain a comparable larval density between trials.

On all trial days, a random sample of 25 larvae was removed from the main population and euthanized with tricaine methanesulfonate (MS-222). Total length was measured for each larva with an ocular micrometer to the nearest 0.1 mm. Mean TL from these larvae was used as the larval length for each trial tank on that day. Data from this experiment were predator capture success, defined as the number of successful strikes divided by total strikes, for each tank.

We used these data to test for a significant relationship between capture success and predator–prey size ratio. We also wished to establish whether this relationship differed among predator species. The predator–prey size ratio was selected as a measure of relative size in this study because it had been used previously to describe a general relationship between relative size and probability of capture for larval prey (Miller 1988), which was used in this study as a candidate function for the model. Two model functions were tested for best fit with a least squared deviation method and compared with a coefficient of multiple determination adapted to account for differences in the number of parameters in a particular model function (R_a^2; Neter et al. 1990). The parameter-weighted R_a^2 is comparable to the Akaike's Information Criterion (AIC) parameter for comparing nonnested models but allows for a clearer interpretation of absolute model fit than is possible with AIC. The first model function was a logistic regression, which has two parameters and is a generally accepted approach for analysis of binary-type data such as capture success (Pampel 2000). The second model function was an inverse negative exponential model that has three parameters and has been used to describe a general relationship between predator–prey relative size and capture efficiency for larval prey (Miller 1988). The logistic model was fit to the data with the logistic procedure in SAS (2002). The Miller model was fit to the data in the NLIN procedure with the Marquardt method of nonlinear estimation (SAS 2002). For both analyses, data were weighted by the number of strikes observed in each replicate. Both models were fit to data for all predators combined and also for each predator species separately. We chose the best model fit for the data based on which modeling approach (logistic vs. Miller and all data vs. predator-specific) resulted in the highest R_a^2 values. For the predator-specific models, we also examined differences in the size-vulnerability relationship among predators based on changes in the model parameter estimates among predators.

Condition-dependent selection

Twelve 589 L round experimental tanks were set up in two sets of six and were visually isolated behind a black plastic curtain. At the beginning of the acclimation period, 10 yellow perch (144–157 mm TL) were placed in each of the six tanks in the first set and 20 alewives (110–180 mm TL) were placed in each of the six tanks in the second set. The TL of each predator was measured to the nearest 1 mm before this introduction. Predators were then allowed to acclimate to the trial tanks for 7 days. This acclimation period included the introduction of yellow perch larvae as a food source to re-acclimate the predators to live food. Predators were otherwise not disturbed except to remove any dead fish. All feeding ceased 24 h before the experimental period.

On the same day that predators were moved into the trial tanks, 500 yellow perch larvae were removed from the main population and split between two 47 L aquaria. Temperature in the aquaria was maintained at 17 °C with a flow of

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0.3 L·min^{-1}. These larvae were fed a ration similar to that of the main population and were allowed to acclimate for 2 days; they were then starved for the remaining 5 days prior to trials. A 5-day starvation period caused a significant decline in larval nutritional condition without 100% mortality (Heyer 2000). On several occasions during the starvation period, cannibalism by larger larvae on their smaller conspecifics was observed. To maintain a representative starved group, all cannibals were excluded from the trials.

During this 5-day starvation period, otoliths of the starved larvae were marked with alizarin complexone (Letcher et al. 1996*b*). To minimize larval mortality resulting from excessive handling or an interruption of flow in the aquarium, the alizarin was introduced to each aquarium at 25 mg·L^{-1} and flow was adjusted so that the alizarin was slowly diluted out of the system over 12 h. In preliminary trials, this protocol resulted in a reliable mark being placed on otoliths that could be used for identification (R.S. Fulford, unpublished data).

On each trial day, a random sample of 25 starved, alizarin-marked larvae (hereafter "starved larvae") were combined in a glass beaker with a random sample of 25 larvae from the main population that had been fed normally during the acclimation period. A trial was started by introducing this mixed group of larvae into one of the 12 experimental tanks selected at random. The predators in this tank were then allowed to feed for 30 min to 1 h. The length of each trial was adjusted to insure a minimal amount of feeding activity but to stop the trial before excessive feeding masked the selective signature (i.e., predators may "select" a larval type first but then continue eating, thereby eliminating evidence of selection). The target was a maximum of 50% consumption per trial. Trials were limited to 1 h or less based on data suggesting larval yellow perch become hard to identify in predator guts after 1.5–2 h (Fulford 2003). All trials were observed to make these adjustments.

At the end of the feeding period, the predators were immediately removed from the tank and euthanized with MS-222. They were then placed on ice and their guts were removed and preserved in 95% ethanol for analysis. This procedure was repeated for each trial tank in random order. On each trial day, 25 larvae from both the main population and from the starved subgroup were euthanized in MS-222 and their total length was measured to the nearest 0.1 mm with an ocular micrometer. These data were used to calculate mean and standard deviation of larval size for each trial tank on that day. Experimental trials were conducted for larvae at 15, 30, 45, and 60 dph.

In the lab, all larvae were removed from the guts, and both sagittal otoliths were removed from all ingested larvae. These otoliths were observed immediately for an alizarin mark, which is clearly visible on freshly removed otoliths. The numbers of larvae with marked and unmarked otoliths consumed in each trial tank were analyzed for differences in percent occurrence of starved larvae in the guts with a Chi square analysis (Neter et al. 1990).

Alternative prey

Twelve 589 L round tanks were used in all trials involving alewife as a predator (hereafter "alewife tanks"), and twelve 147 L rectangular tanks were used in all trials involving yellow perch as a predator (hereafter "perch tanks"). The use of different tanks was a compromise based on available space and previous observations regarding tank type and predator acclimation success. Both tank sets were visually isolated behind black plastic curtains.

Twenty alewife (110–180 mm TL) or eight adult yellow perch (144–157 mm TL) were placed in each tank within the respective sets and were maintained at 17–18 °C with constant flow throughout the acclimation and experimental period. Flow in both tank types was maintained to allow for four complete exchanges of water per day. During the 7-day acclimation period, predators were not disturbed except to remove any dead fish. They were fed yellow perch larvae twice per day during the acclimation period to recondition them to a live food source. All feeding stopped 24 h before the beginning of experimental trials. Tanks within each species block were randomly assigned to one of six possible treatments (zooplankton present or absent × larval density 0.02, 0.09, or 0.16 mg·L^{-1}).

Zooplankton used as alternative prey were collected once per week in Lake Nagawicka (surface area 3.7 km^2, mean depth 11 m), an inland lake located about 30 miles west of Lake Michigan near Milwaukee, Wisconsin. Zooplankton were collected by towing a 0.5 m diameter, 64 μm mesh plankton net 1 m below the surface for 10 min at a site in the middle of the lake (site depth 30 m). Zooplankton was maintained in the laboratory with mild aeration until needed for experiments. Zooplankton represents the major component of the pelagic prey field and, as such, is the only significant alternative prey item to larval yellow perch in the pelagic zone of Lake Michigan, including other larval fishes (Fulford 2003).

Collected zooplankton was filtered at 300 μm to remove small zooplankton from the assemblage before its use as alternative prey. Before the beginning of experimental trials, a mass–density relationship was established for the filtered zooplankton to ease the process of standardizing zooplankton density between trials. This mass–density relationship was established by weighing out standard aliquots of zooplankton on a 64 μm filter and then counting the zooplankton in each aliquot under a dissecting microscope. Zooplankton density was set at 100 organisms·L^{-1} for all trials in the experiment. The mass–density relationship was calculated three times during the experimental period to adjust for any changes in zooplankton species composition.

Trials were initiated by introducing prey into the tank according to treatment. For tanks receiving only larvae, the required number of larvae was poured into a length of PVC pipe plugged with a rubber stopper mounted on a plastic rod. The pipe was lowered slowly into the tank until the bottom reached a depth of about 20 cm, and the larvae were introduced by forcing the stopper downward with the rod. For tanks receiving a mixture of larvae and zooplankton, a preweighed aliquot of zooplankton was added to the tube along with the larvae, and introductions to the predator tank were done in a similar fashion. Trials were conducted one tank at a time in random order. Once prey were introduced to a tank, predators were allowed to feed for a preset period (30 min for alewife and 45 min for adult yellow perch). At the end of the feeding period, all predators were immedi-

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ately removed from the tank and euthanized with MS-222. They were then placed on ice and their guts were removed for analysis. On each trial day, 25 larvae were removed from the main population, euthanized in MS-222, and measured to the nearest 0.1 mm TL with an ocular micrometer. These length data were used to calculate mean and standard deviation for larval size on that trial day. Trials were conducted for larvae at 15 dph (mean TL ± SD = 7.45 ± 63 mm), 30 dph (9.7 ± 1.1 mm), and 45 dph (16.4 ± 2.3 mm).

In the lab, all larvae and zooplankton were removed from predator guts and counted. Data consisted of total number of larvae and zooplankton consumed per minute in each tank divided by the number of predators in the tank. Data were analyzed for a significant difference in feeding rate on either larvae or zooplankton between treatments and larval sizes. Statistical comparisons for a difference in feeding rate on larvae between larvae-only and zooplankton–larvae mixed treatments were conducted with the Wilcoxin rank sum test. Comparisons for a difference in feeding rate on larvae and zooplankton between different larval densities were conducted with the Kruskal–Wallis test. Nonparametric tests were used because of heteroscedasticity caused by high feeding variability between individual predators and low sample sizes within treatments (Hollander and Wolfe 1999).

Individual-based model

The individual-based model was based on a general IBM describing size-selective predation on fish larvae (Letcher et al. 1996*a*). We adapted this model to account for multiple predators based on the approach of Cowan et al. (1996), and where appropriate, we changed their general model functions to functions specific to larval yellow perch based on our laboratory experiments and data from the literature.

This model describes daily predation vulnerability of individual yellow perch larvae as a function of the relative size of predator and prey (Fig. 1). Key parameters are expected daily encounter rate between a predator of size l and the ith larva ($E_{i,l}$) and a size-based probability of attack and capture of a predator of size l and species k on the ith larva ($p_{k,i,l}$). Expected daily encounter rate is based on equations derived by Gerritsen and Strickler (1977) and adapted for a non-trivial prey size by Breck and Gitter (1983). Expected daily encounter rate (number·day^{-1}) is calculated in the model based on reactive distance (cm) of both predator (R_p) and prey (R_L) and relative swimming speed (cm·s^{-1}) of both predator (v) and prey (SS):

$$(1) \qquad E_{i,l} = \pi(R_p + R_L)^2 \cdot \frac{SS^2 + 3v^2}{3v} \cdot \text{Den} \cdot \text{Time}$$

where R_p is equal to 0.8 × predator length (Cowan et al. 1996), and R_L is equal to 2 × larval length·π^{-2} (Bailey and Batty 1983). Larval swimming speed was calculated as a function of larval size based on laboratory observations of larval yellow perch (Houde 1969). Encounter rate is nearly constant with respect to the swimming speed of larval prey because predator swimming speed is so much higher over the range of relative sizes in the model. For eq. 1, predator density (Den) is equal to 10^{-9}, where the denominator is the modeled water volume (mL). Because Den equals the density of a single predator in the modeled volume of water, eq. 1 results in the daily encounter rate between an individual predator (randomly assigned species and length on each model day) and the ith larva (Cowan et al. 1996).

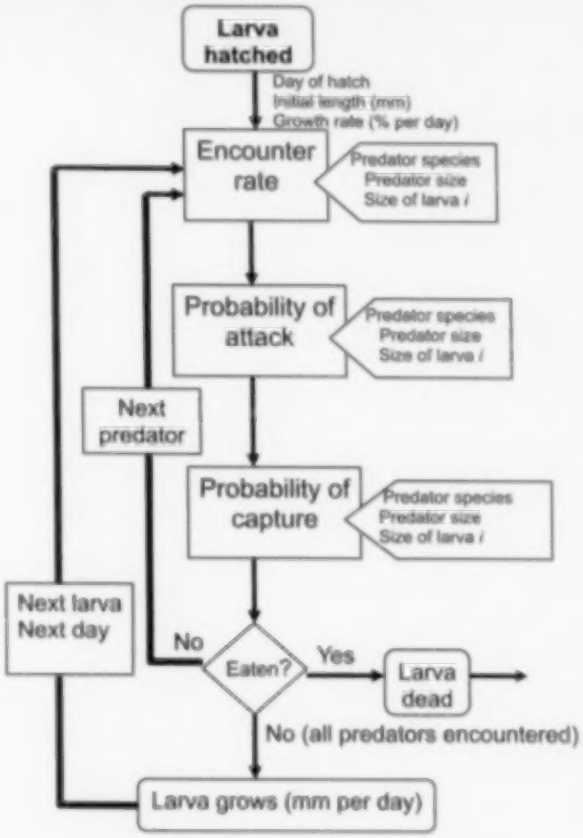

Fig. 1. Flow chart summarizing the predator–prey individual-based model used for the numerical experiments.

Modeled water volume was based on dividing the 10 000 larvae used in the model by mean larval density (number·mL^{-1}) from field data for southern Lake Michigan and Green Bay (1 × 10^{-5}·mL^{-1}). We arbitrarily chose to use an initial larval population size of 10 000 because this number was high enough to allow sufficient survivors for analysis without resulting in excessive model run time. Actual number of predators in the modeled volume was based on density data from midwater trawls and hydroacoustic analyses at several sites around Lake Michigan (30–60 fish·1000 m^{-3}; Fabrizio et al. 1997) and adjusted within their range in our model to achieve survival from 1% to 2% over the 45-day model period. Equation 1 was calculated separately for each predator on a given model day.

Encounter rate was converted to expected encounters per day by multiplying by total daily feeding time (Time, 42 300 s). This value is based on predation occurring only during the 12-h daylight period. This is based on the observation that yellow perch larvae are only active (i.e., vulnerable to predation) during the day and represents a simplification for modeling. Actual predator activity is often

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condensed into shorter periods (e.g., dawn and dusk); however, for a comparison of vulnerability with size, this is a reasonable simplification (Cowan et al. 1996; Letcher et al. 1996*b*). Realized daily encounter rate between the *i*th larva and a predator of size *l* ($ER_{i,l}$) is drawn randomly in the model from a Poisson distribution with $E_{i,l}$ as the rate parameter. Encounter rate did not change among predator species.

The daily probability of attack and capture ($p_{k,i,l}$) for a predator of species *k* and length *l* in the model was a function of predator–prey size ratio defined empirically based on our laboratory results:

$$(2) \qquad p_{k,i,l} = CS_{k,i,l} \cdot a_{k,i,l}$$

where $CS_{k,i,l}$ is the capture success given an attack on the *i*th larva by a predator of species *k* and length *l*, and $a_{k,i,l}$ is the relative attack rate on the *i*th larva by a predator of species *k* and length *l*.

We used the results from the capture success experiment in two ways. First, we used these data to build a predictive function for capture success based on the predator–prey size ratio. This predictive function was the best-fit equation resulting from the capture probability analysis mentioned previously. Second, we used results from the capture success experiments in the form of number of strikes per trial (both successful and unsuccessful) to develop a functional relationship between predator relative probability of attack ($a_{k,i,l}$) and predator–prey size ratio. This approach rests on the assumption that the number of attacks observed in a fixed period is an index of the relative probability of attack based on relative size of predator and prey. We can only estimate relative probability of attack because our experimental results cannot account for tank size effects on encounter rates or for differences in encounter rate between our experimental system and Lake Michigan.

We tested for a significant relationship between probability of attack and predator–prey size ratio for each predator type and whether the slope of these relationships differed from zero using a simple linear regression analysis (SAS 2002). Probability of attack was set at 0.5 by Letcher et al. (1996*a*) for a general predator in order to achieve reasonable larval mortality rates in their model. We adapted this approach to allow the probability of attack to vary around a preselected mean value (0.5) based on the probability of attack–size ratio relationship established in our experiments. These two functions combined ($CS_{k,i,l} \times a_{k,i,l}$) allowed us to incorporate size- and predator-specific differences in both attack rate and capture success into our model.

Daily vulnerability of the *i*th larva to a predator of species *k* and length *l* ($V_{k,i,l}$) is defined as the probability of an individual larva not escaping all its encounters with that predator, based on a binomial probability function:

$$(3) \qquad V_{k,i,l} = 1 - (1 - p_{k,i,l})^{ER_{i,l}}$$

where the number of trials is the realized daily encounter rate ($ER_{i,l}$) and the success probability is the probability of attack and capture ($p_{k,i,l}$). Vulnerability for each larva on each day was compared with a uniform random number (x) between 0 and 1, and if $V_{k,i,l}$ was more than x, then the *i*th larva was removed from the simulation.

Numerical experiments

The predator–prey IBM was used to address questions regarding the influence of differences in individual DOH on size-dependent predation vulnerability of larval yellow perch. All model runs lasted 45 days based on the estimated length of the pelagic larval period for yellow perch (30–40 days). All numerical experiments were run with an initial cohort of 10 000 larvae, which were introduced into the model gradually over the first 24 days of each model run. The number of individual larvae that entered the model each day was $b_d \times 10\,000$, where b_d is a value between 0 and 1 taken from a DOH frequency distribution based on observed hatching patterns for yellow perch in Lake Michigan (Fulford 2003). Both initial size and individual growth rate were randomly assigned to each larva at the beginning of the model run based on respective normal distributions. The mean and variance of initial larval size (mean ± SD, 5.7 ± 0.13 mm) were based on hatch size data collected in the laboratory (R. Fulford, unpublished data). The mean and variance for larval growth rate were manipulated as a part of the numerical experiments (see below). Therefore, size variability for larvae in the model reflected the combined effects of variation in initial size, growth rate, and timing of hatch. Each numerical experiment consisted of three replicate model runs to account for model stochasticity.

First, we investigated how DOH distributions of survivors are affected by changes in size variability within cohorts caused by interannual changes in mean growth rate. Previous research has shown that changes in mean growth rate between cohorts can result in changes in the size dependence of larval vulnerability to predation (Cowan et al. 1996; Rice et al. 1993), and we wished to investigate how these changes are reflected in the DOH distribution. We conducted model runs at two mean growth rates (2% and 4% per day, SD 0.1% for both) representative of the range of mean growth rates we observed for larval yellow perch in Lake Michigan. We also conducted model runs in which larvae were exposed to mortality of a similar magnitude that was independent of larval size. These three scenarios were hypothesized to result in a range of size dependence, measured as the daily mean difference in length between survivors and nonsurvivors. We further hypothesized that these differences in the size dependence of mortality would be reflected as differences in the DOH distribution pattern of survivors. Output for the growth rate variability experiment was cohort survival, daily mean length of survivors and nonsurvivors, and DOH distribution of survivors. Simulations were conducted for each predator type (alewife, white perch, and adult yellow perch) to assess predator-specific differences in size selectivity. Predator density was set at 0.045 predators·m^{-3} based on mean density data for predators in Lake Michigan (Fabrizio et al. 1997).

The second numerical experiment addressed how patterns in survival and DOH distribution of survivors were affected by a simulated predation pulse. Increased vulnerability to mortality was simulated with a five-day period of predation occurring at different times throughout the larval period (days 0–5, 6–10, 11–15, 16–20, 21–25, 26–30, 31–35, 36–40, and 41–45). Predator density during the predation pulse was 0.045 m^{-3}, and mean larval growth rate was set at 4%

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per day (SD 0.1% per day) for all simulations. Output for the timing of predation experiment was total larval survival and DOH distribution of survivors for each model run.

Results

Probability of capture

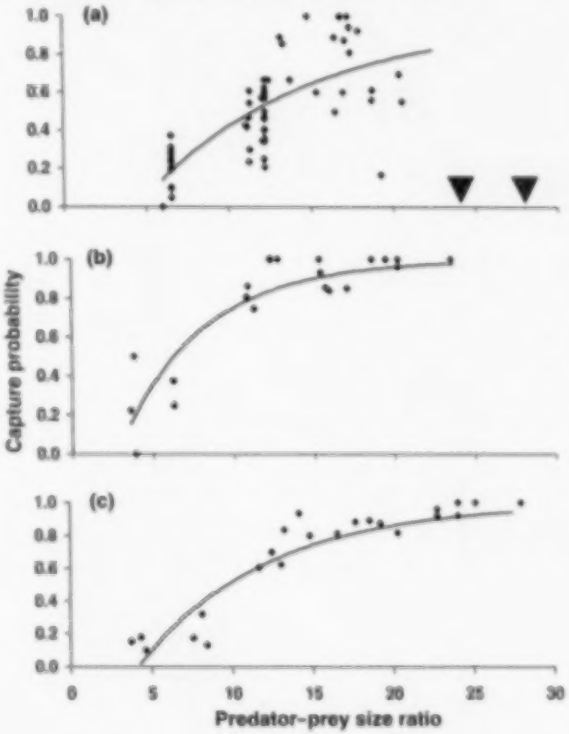
Capture success of individual predators feeding on larval yellow perch varied with predator–prey size ratio for all predator species tested (Fig. 2). Capture success was low for the smallest size ratios and rose monotonically with increasing size ratio. For white perch and yellow perch predators, maximum capture success was achieved around a predator–prey size ratio of 12–14 and remained high for all larger size ratios tested. Trials that involved predation by alewife at larger size ratios (i.e., smallest larvae) resulted in no attacks. As a consequence, alewife displayed an ascending pattern similar to those of the other two predators at lower size ratios but no evidence that capture probability was maximized over a wide range of size ratios, as was indicated for white perch and adult yellow perch. Capture probability also differed in variability between predator species. Maximum observed capture probability was high for all three predator species (alewife, 1.0; white perch, 1.0; yellow perch, 0.94); however, the observed values for alewife were much more variable than for the other two species.

We used these data for capture success as a function of predator–prey size ratio to develop a predictive relationship that could be used in the individual-based model. The logistic model performed better than the Miller model when both functions were fit to the data for all three predators combined, but the R^2 value for both models was generally low (Table 1). However, model fit was noticeably improved when data for each predator species were fit separately, which suggests the capture success – size relationship differs between species. Further, R_a^2 values were higher for the species-specific fit of the Miller model for all three predators compared with the species-specific fit for the logistic model (Table 1). Based on a comparison of parameter estimates for the predator-specific Miller model, differences in the relationship between capture success and relative size among predators are largely due to differences between alewife and white perch, with values for all three parameters for adult yellow perch falling between those of the other two predators (Table 1; Fig. 2). Given these results, we used the predator-specific Miller model to predict capture success as a function of predator–prey size ratio for each predator species in the model simulations.

Relative probability of attack

Predator interest measured as the number of strikes (successful and unsuccessful) observed in each 30-min trial also differed among predator species (Fig. 3). Predator interest of alewife feeding on yellow perch larvae declined significantly with increasing size ratio (strikes = −1.2(size ratio) + 33.2; t test, $p < 0.001$). In contrast, white perch showed a positive linear relationship between predator interest and size ratio; however, the slope of this relationship did not differ from zero (strikes = 0.44(size ratio) + 8.3; t test, $p = 0.18$). Adult yellow perch showed no detectable change in their interest

Fig. 2. Capture success measured as the number of successful captures/number of strikes for (*a*) alewife (*Alosa pseudoharengus*), (*b*) white perch (*Morone americana*), and (*c*) adult yellow perch (*Perca flavescens*) feeding on larval yellow perch. The diamonds are experimental data and the line is the best fit of the Miller model. Black triangles on the alewife chart indicate size ratios at which all trials resulted in no attacks.



over the tested range of size ratios (strikes = 0.09(size ratio) + 19.4; t test, $p = 0.62$).

These data were used to adapt a general probability of attack parameter for predators preying on larval fishes into a size-based function that varied in shape among predator species but had the same mean value. A function describing relative probability of attack ($a_{k,l,l}$) for the ith larva by all predators encountered of species k and size l was constructed by assuming relative probability of attack will be zero at size ratios where no strikes were observed and maximum probability of attack would occur at size ratios where the maximum number of strikes was observed for each predator species. Finally, the overall mean value of $a_{k,l,l}$ across all predators and size ratios was set to 0.5 for all simulations. The conversion of strikes data to $a_{k,l,l}$ took the following general form:

$$\text{strikes} = m(\text{size ratio}) + b \quad (4)$$

$$a_{k,l,l} = (1/\max_k)\,\text{strikes} \quad (5)$$

where strikes equals the number of strikes in 30 min predicted based on the experimental data for a predator of species k and length l, and $\max_k$ is the maximum number of

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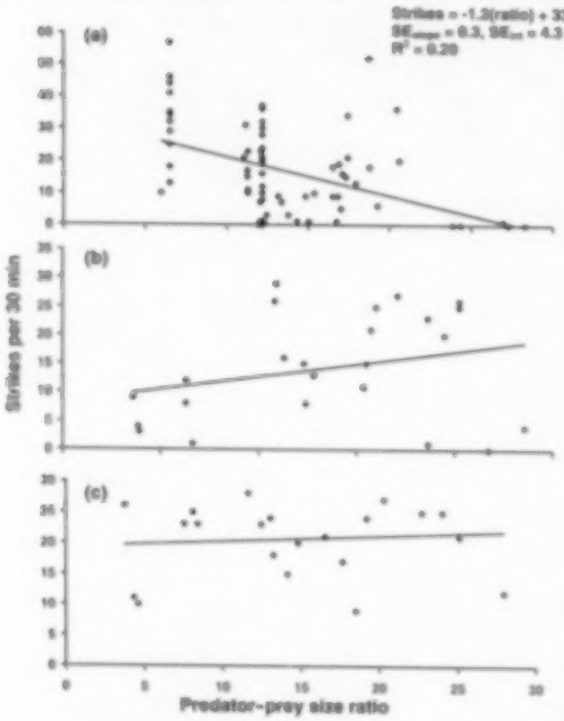
Table 1. Results of model fit for the logistic model and the Miller model for capture probability as a function of predator–prey size ratio from laboratory experiments.

Model type	Model formula	Modeled data	α	β	R^2	R_a^2
Logistic model	$P(\text{capture}) = e^{\text{logit}}/(1 + e^{\text{logit}})$	All predators	−2.62 (0.15)	0.23 (0.01)	0.62	0.62
	logit = $\alpha + \beta$ ratio	Alewife	−2.42 (0.03)	0.18 (.003)	0.49	0.48
		White perch	−1.50 (0.13)	0.25 (0.01)	0.81	0.8
		Adult yellow perch	−2.88 (0.07)	0.26 (0.005)	0.85	0.85
Model type	Model formula	Modeled data	β_1	β_2	R^2	R_a^2
Miller model	$P(\text{capture}) = \dfrac{100 - [(\text{ratio} + \beta_1)/\beta_2]^{-\beta_1}}{100}$	All predators	452.2 (4.7)	500 (0.5)	49.2 (6.1)	0.6	0.59
		Alewife	453.2 (80.8)	510.2 (89.0)	41.7 (0.6)	0.52	0.5
		White perch	180.9 (40.4)	204.9 (44.6)	35.7 (1.4)	0.85	0.83
		Adult yellow perch	325.4 (37.3)	367.3 (41.3)	40.2 (0.6)	0.92	0.91

Note: Each model was fit to the entire data set (all predators) and to data for each of the three predator species separately. Values in parentheses next to model parameters are the standard error for that parameter estimate. The value "ratio" in the model formula is predator–prey size ratio. R^2 values are the unweighted coefficient of multiple determination and the R_a^2 values are weighted by the number of parameters in the respective model (Neter et al. 1990). The Miller model predicts a negative capture probability for predator–prey size ratios below a critical value (−3.1), and capture probability was set to zero in the model for size ratios below this value.

Fig. 3. Predator feeding interest defined as the total number of strikes made in 30 min as a function of predator–prey size ratio (ratio) by (*a*) alewife (*Alosa pseudoharengus*), (*b*) white perch (*Morone americana*), and (*c*) adult yellow perch (*Perca flavescens*) feeding on larval yellow perch. The diamonds are experimental data and the line is a best-fit linear function. The best-fit linear function, standard error for the slope (SE_{slope}) and intercept (SE_{int}), and R^2 are given for significant trends.



strikes predicted for a predator of species *k*. This relationship is based on the assumption that under constant conditions changes in predator interest with predator–prey size ratio reflect changes in relative probability of attack as a function of relative size. Only the strikes per trial – size ratio function for alewife displayed a slope significantly different from zero, so alewife relative probability of attack changed with size in the model. Relative probability of attack for white perch and adult yellow perch was set to 0.5.

Condition-dependent selection

Mean length of larvae did not differ between the starved and fed treatment groups (*t* tests, $p < 0.02$ all dates; Table 2). Across all trials used for analysis, predators consumed an average of 37% (10%–60%) of larvae in an individual trial. In most cases, both alewife and adult yellow perch showed no significant selection for or against starved larvae (Fig. 4). The only exception was that alewives captured starved larvae more often than unstarved larvae at 30 dph when predator–prey size ratios were between 11 and 14, which is near the optimal size ratio for attack and capture for alewives ($\chi^2 = 5.89$, 1 df, $p < 0.03$). We did not detect significant condition-dependent selection by alewives at any other size ratio. Yel-

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Table 2. Summary data for mean total length (mm) of larvae used in the condition-dependent selection experiment.

Larval age, days after hatch	*n*	Mean total length (range)		
		Fed larvae	Starved larvae	*p* value
15	25	8.7 (8.0–10.1)	8.6 (7.9–10.0)	0.52
30	25	12.7 (11.4–14.4)	12.2 (11.4–13.1)	0.23
45	25	20.2 (14.1–24.4)	20.1 (14.6–24.1)	0.95
60	25	36.6 (27–46)	33.4 (26–41)	0.21

Note: Data are presented separately for the starved and fed treatment groups and *p* values are given for a *t*-test testing for differences in mean length between treatment groups.

Fig. 4. Probability (±1 standard error) that a larva captured by either alewife (*Alosa pseudoharengus*; solid bars) or adult yellow perch (*Perca flavescens*; open bars) in mixed-condition prey experiments was starved. Trials were conducted at 15, 30, 45, and 60 days after hatch. Mean total length of larvae in each age treatment is given in parentheses. The reference line at 0.5 indicates random selection; however, statistical results reported are based on a chi-square analysis.

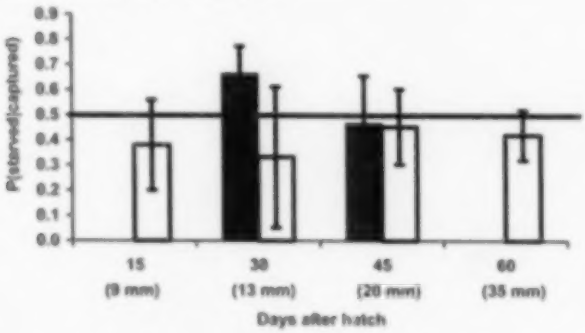
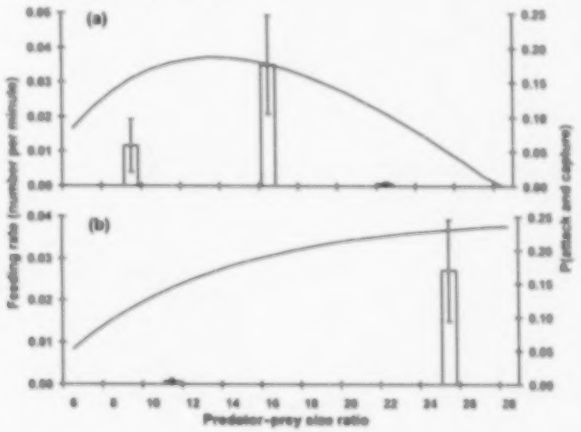


Fig. 5. Probability of attack and capture estimated from capture success experiments (line) and feeding rates measured in the alternative prey trials (bars; ±1 standard error) for (*a*) alewife (*Alosa pseudoharengus*) or (*b*) adult yellow perch (*Perca flavescens*) feeding on larval yellow perch. Feeding rates are the combined mean of zooplankton-present and zooplankton-absent trials conducted at each predator–prey size ratio.



low perch displayed no significant condition-dependent selection at any size ratio tested ($\chi^2 < 3.4$ all sizes, 1 df, $p > 0.05$).

Alternative prey selection

Both alewife and adult yellow perch fed during this experiment on both larval yellow perch and zooplankton. Zooplankton used as alternative prey consisted of more than 70% copepods with the remainder a mix of large and small cladocerans. Alewives fed consistently on zooplankton, but feeding rate showed no trend with larval biomass (Kruskal–Wallis $H = 0.52$, $p > 0.3$). Feeding rate for adult yellow perch on zooplankton was low, occurring in only two out of 18 trials, with no trends evident in these data as a function of larval biomass.

Feeding rates (larvae per minute) as a function of size ratio for both predators were consistent with results from the capture success experiments. We observed maximum feeding rate in this experiment at about the same size ratio at which we would predict maximum probability of attack and capture based on the results of the capture success experiment (Fig. 5). A positive functional response was observed for alewife feeding on larval yellow perch (Fig. 6); however, this result was not statistically significant (Kruskal–Wallis $H = 0.92$, $p > 0.2$). The presence or absence of alternative prey did not significantly affect alewife feeding rates on larvae (Wilcoxin statistic 0.63, $p > 0.05$). We did not observe any trend in functional response for adult yellow perch feeding on larvae (Fig. 6; Kruskal–Wallis $H = 0.52$, $p > 0.3$). However, the feeding rate of adult yellow perch on larvae was 2–3 times higher in the presence of alternative prey than without alternate prey (Fig. 6; Wilcoxon statistic 1.8, $p < 0.05$).

Numerical experiments

Growth rate variability and predator species comparison

Vulnerability of larval yellow perch to predation generally increased with predator size and decreased with increasing larval size. The shape of these relationships shifted among predator species in accordance with predator-specific differences observed in the capture probability experiments. Vulnerability of larval yellow perch to both white perch and adult yellow perch rose monotonically as a function of predator size and was near the maximum vulnerability at a predator size of 160 mm TL for all larval sizes tested (Fig. 7). However, at predator sizes below 160 mm TL, larval vulner-

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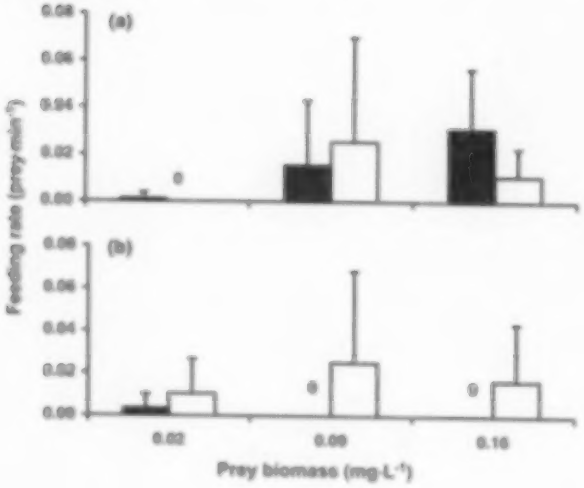
Fig. 6. Feeding rate for (*a*) alewife (*Alosa pseudoharengus*) and (*b*) adult yellow perch (*Perca flavescens*) on larval yellow perch at three larval densities (0.02, 0.09, and 0.16 mg·L^{-1}): solid bars, zooplankton-absent treatments; open bars, zooplankton-present treatments. Zeros on graph indicate treatments where no predator feeding occurred.



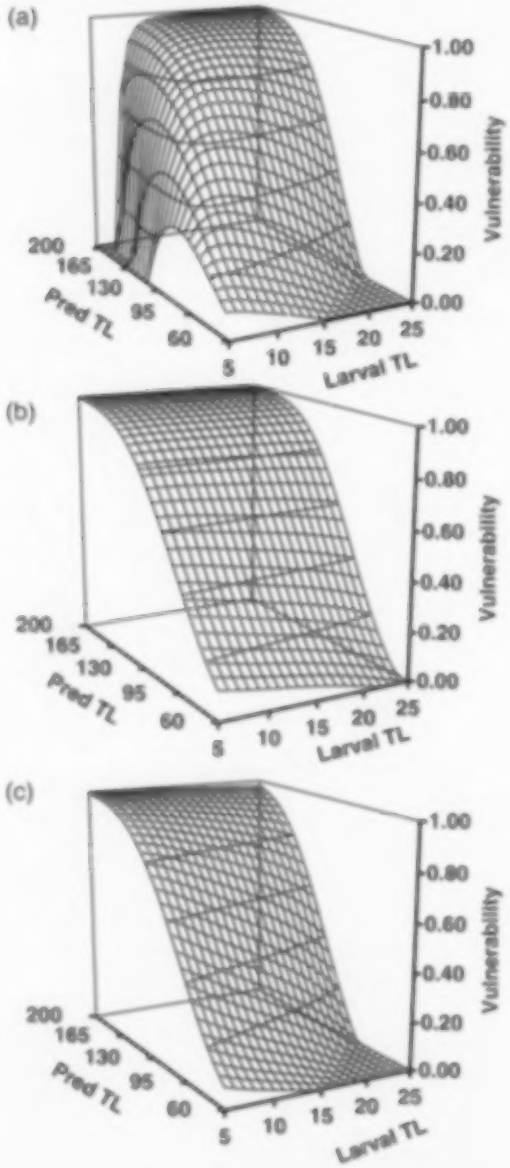
ability to predation dropped rapidly with increasing larval size when the predator was either alewife or adult yellow perch. In contrast, the slope of the relationship between vulnerability and larval size when the predator was white perch was much shallower, suggesting that larval yellow perch grow out of the vulnerability window to predation by white perch more slowly and larvae are likely to remain vulnerable to white perch for more of the larval period.

Larval vulnerability to alewife predation was more parabolic in nature than vulnerability to white perch or adult yellow perch with a size refuge evident for both the smallest and the largest larvae (Fig. 7). Larval vulnerability to predation by alewife was maximized for the smallest range of predator and larval sizes, and larval vulnerability to alewife dropped much more rapidly as larvae grew than did vulnerability to white perch or adult yellow perch. Of the three predators, vulnerability to predation by alewife appears the most strongly dependent on larval size.

At comparable predator densities, larval yellow perch survival over 45 days was lowest with white perch as predators (mean survival (S) = 0.007) and highest with alewife as predators (S = 0.02) across both growth rates tested. However, these differences in survival among predators did not translate into measurable differences in the size or DOH distributions of larval survivors (Kolmogorov–Smirnov test, p > 0.1 for size and DOH). Survival rate also changed as a function of larval growth rate. Mean survival over 45 days was lower at the low growth rate (2% per day; S = 0.008) than at the high growth rate (4% per day; S = 0.018) across all predator types.

The outcome of size-dependent predation, measured as the maximum difference in mean length between larval survivors and nonsurvivors, did not differ noticeably among predators but increased in response to increases in mean

Fig. 7. Larval yellow perch (*Perca flavescens*) vulnerability to predation as a function of both predator total length (Pred TL, mm) and larval total length (Larval TL, mm) for (*a*) alewife (*Alosa pseudoharengus*), (*b*) white perch (*Morone americana*), and (*c*) adult yellow perch as predators. Surface plots are based on a deterministic calculation of model functions.



growth rate (Fig. 8). As expected, nonselective model runs showed no size difference between survivors and nonsurvivors. Maximum size difference (mean across all predators) increased to 1.3 mm at a mean growth rate of 2% per day and 6.5 mm at 4% per day. Length differences between survivors and nonsurvivors became positive around day 25 independent of changes in mean growth rate. These results are consistent

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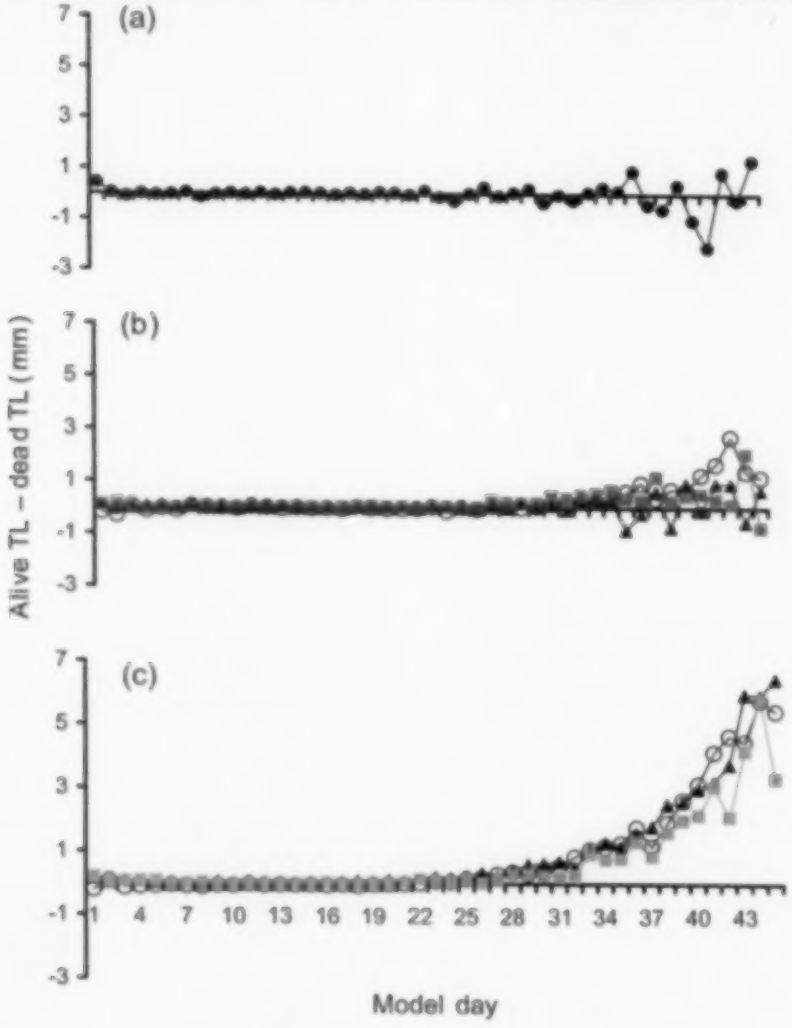
Fig. 8. Daily mean difference in total length (TL) between survivors (alive TL) and nonsurvivors (dead TL) for larval yellow perch (*Perca flavescens*) resulting from model runs ($n = 3$ per treatment) conducted with (*a*) size-independent mortality and (*b* and *c*) size-dependent mortality at a mean larval growth rate of (*b*) 2% per day and (*c*) 4% per day. Results are given for simulations run separately for alewife (*Alosa pseudoharengus*; circles), white perch (*Morone americana*; triangles), and adult yellow perch (squares).



with prior IBM analyses of larval vulnerability to predation (Cowan et al. 1996; Rice et al. 1993) based on size and demonstrate that the model is appropriately describing a range of intensity for size-selective predation against which we can compare patterns in the DOH distribution of survivors.

Observed changes in the DOH distribution of larval survivors on model day 45 (i.e., end of the larval period) were associated with observed changes in size selectivity. Mortality in the model that was not size selective resulted in a hatch date distribution favoring later-hatched larvae by the end of the larval period because of their shorter duration of exposure to mortality (Fig. 9). We observed minimal difference between the DOH distribution of survivors subjected to size-dependent predation at a larval growth rate of 2% per day and the DOH distribution of survivors subjected to mortality that was not size-dependent. In contrast, when the growth rate of the larval cohort was raised to 4% per day, the DOH distribution of survivors more closely resembled the initial DOH distribution.

However, a more detailed examination of DOH distributions over the simulation period revealed a more complex pattern. On model day 25, the DOH distributions of survivors were similar among the three scenarios (non-size-selective, low growth, and high growth), shifted somewhat to a later DOH. In fact, it appears that it was only in the later larval period between day 25 and day 45 that DOH distributions in the high growth scenario deviated from the other two, shifting back towards earlier DOH. Day 25 is also close to the

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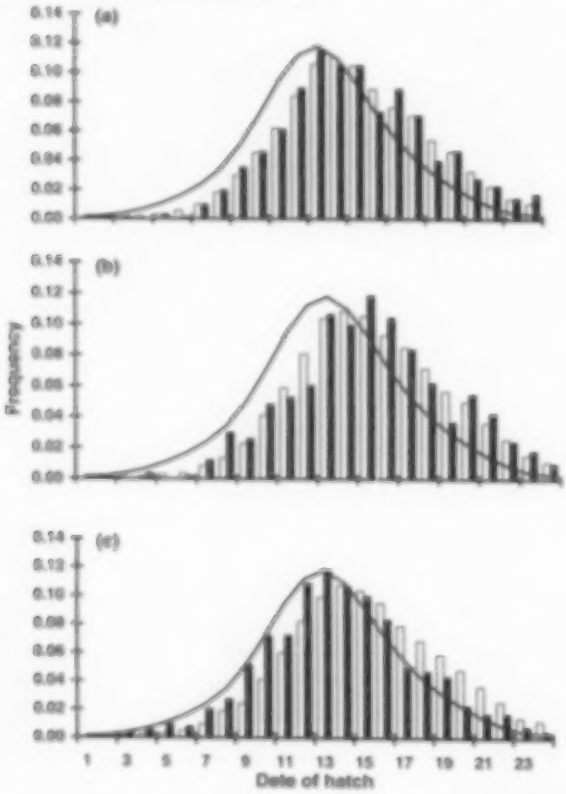
Fig. 9. Date of hatch frequency distribution on model days 25 (open bars) and 45 (solid bars) compared with initial hatch date distribution (line) for (*a*) nonselective mortality simulations and (*b* and *c*) simulations of size-selective predation by alewife (*Alosa pseudoharengus*) with (*b*) low (2% per day) and (*c*) high (4% per day) mean larval growth rate.



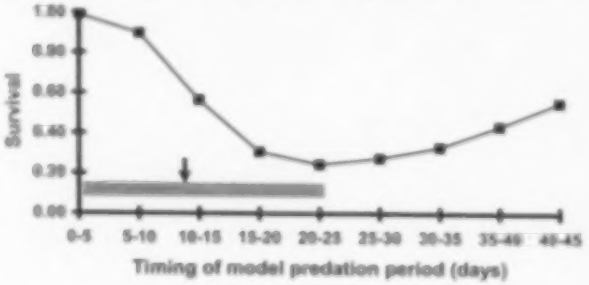
time that size dependence became detectable in individual larval survival (Fig. 8). When growth rate and DOH vary independently, non-size-selective larval mortality seems to favor later-hatched larvae as they have had less exposure to predation, and the onset of size dependence in larval mortality is correlated with a decrease in survival of late-hatched larvae because they are the smallest larvae in the system.

Predation pulse experiment

For an analysis of the effects of a predation pulse on larval survival, we chose to use only alewife as a predator in model simulations. Alewife are of particular interest as a predator of larval yellow perch in several systems, including Lake Michigan. Further, vulnerability of yellow perch larvae to alewife also appeared the most divergent from general vulnerability patterns described previously (Cowan and Houde 1992; Letcher et al. 1996*a*) and, as such, merits closer scrutiny.

The simulated 5-day predation window resulted in DOH distributions of survivors with two basic patterns, depending on how close the predation window was placed to peak hatch. Survival was high when predation was focused during the early-larval period, as most larvae had not yet hatched

Fig. 10. Forty-five day larval survival predicted in model runs simulating a 5-day period of predation occurring at different times throughout the larval period. Hatching period for larval yellow perch (*Perca flavescens*) in the model is indicated by the shaded bar, and peak hatch is indicated by the black arrow.



and fewer larvae were exposed to predation (Fig. 10). When the predation window occurred between day 25 and the end of the simulation, cohort survival once again increased, because as predation occurred later in the larval period, more larvae had reached a size at which size-dependent vulnerability to predation was decreasing.

Timing of predation also affected patterns within the DOH distribution (Fig. 11). Predation during the early hatching period generated little change in the DOH distribution, as most larvae were not available to be captured at this time. When the predation window occurred close to the timing of peak hatch (days 11–15), later-hatched larvae were overrepresented in the final DOH distribution, suggesting a survival advantage for these larvae. When the predation window occurred just after peak hatch (model days 16–20), later-hatched larvae were again overrepresented, but the survival advantage was reduced in comparison to predation around peak hatch. Finally, when the predation window occurred after day 20 in the model, the DOH distribution resembled the initial distribution with no apparent survival advantage as a function of DOH.

Discussion

Predation vulnerability of larval yellow perch is affected by larval and predator size, as well as predator species. Capture probability increased with increasing size ratio for all three predators in laboratory experiments, but unlike that for white perch and adult yellow perch, interest in larval prey by alewife decreased and actually dropped to zero with increased predator–prey size ratio, that is, they ignored small larvae. Larval vulnerability to predation by either white perch or adult yellow perch is largely a function of larval escape capacity, but larval vulnerability to predation by alewife is a function of both larval escape capacity and the probability that alewife will attack. Therefore, vulnerability of larval perch to alewife predation as a function of size is more complex than vulnerability to other fish predators.

Our findings regarding differences in larval capture probability as a function of relative size are affected to some degree by our choice of both a relative size metric and a functional relationship between relative size and probability of larval capture. The model function used to describe the size – capture success relationship was based on a general

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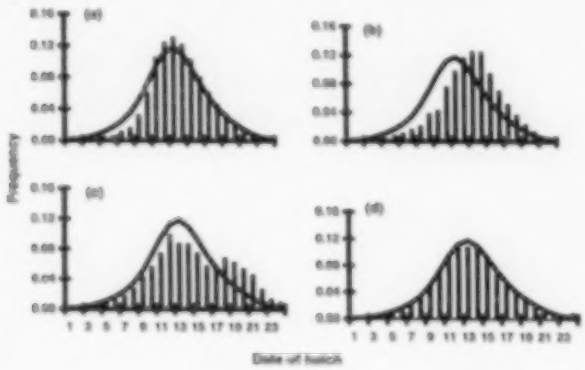
Fig. 11. Initial date of hatch distribution (DOH; line) and DOH frequency distributions of larvae surviving to the end of the larval period (solid bars; model day 45) predicted by the model from simulating a 5-day predation window on model days (*a*) 6–10, (*b*) 11–15, (*c*) 16–20, and (*d*) 21–25. Distributions resulting from predation later in the larval period did not differ from that caused by predation during days 21–25 and therefore are not shown.



function presented by Miller (1988) in their literature review of size-dependent processes to describe a relationship between predator–prey size ratio and larval capture success. No single function will completely describe all of the variability observed in our laboratory data, especially for alewife. However, our objective was to describe general patterns in larval survival between different predators and as a function of larval growth rate and DOH. The Miller model is well suited to these objectives.

Several relative size metrics have been suggested in the literature for describing size-dependent processes in fish predation, including predator–prey size ratio (Miller 1988; Letcher et al. 1996*a*), prey–predator size ratio (Pepin et al. 1992), and prey length – predator gape (Scharf et al. 2000). Measures of predator gape may incorporate differences among predators better than predator length, but no consensus exists on a single most useful metric of predator–prey relative size. We chose the predator–prey size ratio for this analysis because this metric incorporates commonly collected data on fish predators and is easily comparable across broader taxonomic boundaries.

The relationship between predation vulnerability and relative size has been explored previously for larval prey, and the pattern exhibited by white perch and adult yellow perch is similar to patterns described for generic fish predators (Bailey and Houde 1989; Cowan and Houde 1992). Vulnerability was high for newly hatched larvae and dropped slowly with increasing larval size until larvae reached a threshold length, at which point vulnerability dropped rapidly to zero (Cowan et al. 1996; Paradis et al. 1996). In addition, our observed threshold for the transition away from maximum vulnerability occurred at a size ratio close to 10, which is the size ratio of maximum larval vulnerability reported by Paradis et al. (1996) based on their review of the literature.

In contrast, the pattern for alewife did not match these generic patterns for fish predators well. Alewife made no attacks on the smallest larvae. When they did attack, capture efficiency was maximized for only a narrow band of predator–prey size ratio (14–18). Further, alewife were more selective at these size ratios for larvae in poor nutritional condition. Through all of our experiments, alewife showed the highest capture efficiency for larvae when the size ratio was in this range. This is a vulnerability – relative size relationship previously ascribed to raptorial predators and suggests a more complex size–vulnerability relationship for alewife preying on larval fishes than has been observed for other planktivorous fishes (Cowan et al. 1996). Alewife capture efficiency for larval yellow perch likely differs from other planktivores because alewife exhibit behavioral plasticity in feeding behavior in response to prey type and density.

Janssen (1976) described two feeding modes for alewife: particulate feeding and filter feeding. Particulate feeding is hypothesized to be more selective as alewife are choosing prey visually and are more likely to attack larger, more active prey items based on an optimal feeding model (Crowder and Binkowski 1983). Filter feeding is largely not size selective as the alewife are simply collecting all prey in their path and prey are captured or not based largely on their inherent escape abilities. The shift between feeding modes is based on prey density, prey size, and predator size (Janssen 1976).

Similar laboratory studies of other facultative filter–particulate feeders, such as walleye pollock (*Theragra chalcogramma*; Ryer et al. 2002) and herring (*Clupea harengus*; Gibson and Ezzi 1992), demonstrate that switching from filter to particulate feeding as prey become larger and less abundant has energetic advantages as filtering-efficiency drops. However, this switch also appears associated with a switch from mechanosensory to visual foraging (Ryer et al. 2002), which may provide a refuge for larger, less abundant, yet less visible prey like early-stage larval fishes.

Alewife appear to feed on larval yellow perch in a particulate mode most of the time, and the lack of interest shown by alewife for the smallest larvae in our experiments may have resulted from these larvae being visually undetectable to alewife. Alewife do feed in a particulate manner on smaller organisms such as *Daphnia* and mysids; however, these organisms have more pigmentation and rigid body parts that make them more easily detected. It is reasonable to assume that alewife might filter-feed on yellow perch larvae if they were present in sufficient densities, which would increase attacks on smaller larvae.

Alewife behavior also changed as larval density increased. Alewife always fed on larvae at densities above 100 m^{-3}, but they fed intermittently, if at all, below this density. Further, feeding rate was positively associated with larval density when larvae were between 7–9 mm TL. In general, a high level of alewife predation on larval yellow perch is predicted to occur if larvae and alewife interact at or near the optimal size ratio and if larval densities are high. This conclusion is supported by observations of alewife predation on larval yellow perch in other systems. Brandt et al. (1987) documented massive predation by alewife on larval yellow perch in a small embayment adjacent to Lake Ontario. They reported that predation was highest in years when alewife interacted with larvae between 7 and 9 mm TL at a larval density of 79 m^{-3}, but they observed less predation when alewife did not appear until larvae were larger. Moreover, they reported

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that incidence of yellow perch larvae in alewife stomachs declined to less than 1% at a larval density of 11 m^{-3}, despite the larvae being an optimal size. Luecke et al. (1990) also observed that alewife show a positive functional response to larval bloater at densities exceeding 100 m^{-3}, but feeding rate was near zero by alewife at a larval density of 50 m^{-3}.

Larval yellow perch densities this high are rare in Lake Michigan. Larval densities in Green Bay, a shallow, productive embayment of Lake Michigan at the lake's northwest corner, have peaked at 18 m^{-3} in recent years (Brian Belonger, Wisconsin Department of Natural Resources, Peshtigo, Wisconsin, unpublished data), and the maximum density for larval perch from our sampling in the main body of Lake Michigan in 1998–2001 was less than 1 m^{-3} (Fulford 2003). These field densities support the results of our study that alewife predation is likely not a significant limiting factor for yellow perch larval survival at present.

Vulnerability of larval yellow perch to predation by both white perch and adult yellow perch remained high for a wider range of predator–prey size ratios in comparison to alewife. Moreover, larval vulnerability to these predators was not dependent on larval density. White perch and adult yellow perch should affect larval survival over a longer portion of the larval period than alewife and have a more significant effect on year-class strength when these predators are present. However, white perch are not abundant in the main body of Lake Michigan and adult yellow perch are found primarily in deeper water away from the pelagic zone, so these two predators are also not likely to have a strong influence on the survival of larval yellow perch in Lake Michigan. Overlap between larval perch and both white perch and adult yellow perch is likely to be higher in smaller, shallower systems such as Green Bay. Both predators are abundant in Green Bay and the limited depth makes spatial overlap more likely compared with a deeper, more open system like Lake Michigan. At present, predation does not appear to be a significant factor limiting larval yellow perch survival in Lake Michigan.

One interesting finding regarding larval vulnerability to predation by adult yellow perch was that feeding rate of adult yellow perch on larval yellow perch increased if alternative prey were present. Intracohort cannibalism has been reported for natural populations of European perch (*Perca fluviatilis*; Brabrand 1995) and for adult yellow perch feeding on young-of-the-year perch in Oneida Lake, New York (Tarby 1974), but the general importance of cannibalism to recruitment has not been well explored.

Two causes for an increase in feeding rate by adult yellow perch in the presence of alternative prey seem plausible: either adult yellow perch were simply responding to a generic increase in prey density and this was a functional response, or the foraging activity of the larval yellow perch brought on by zooplankton being present made them more vulnerable to predation. It is not possible to draw conclusions regarding the veracity of these two hypotheses from our data because we did not monitor larval activity or examine the guts of larvae to check for feeding activity. However, in all of our trial tanks, only a few adult yellow perch fed on zooplankton and they showed no evidence of a functional response. The fact that adult yellow perch did not show a functional response to an increase in the density of larvae or zooplankton suggests that selectivity for these prey is low and supports the idea that larvae are more vulnerable to cannibalism when actively feeding. Anecdotal observations of feeding behavior during our probability-of-capture experiments indicated that adult yellow perch remain near the bottom of the tank, while larvae occupied the upper third of the tank. This behavioral separation likely contributed to the lack of an observed functional response, as adult yellow perch are preying principally on larvae that "stray" closer to the bottom and the frequency of straying may not change with larval density. As a result, adult yellow perch did not appear to actively search for prey near the surface, and observed attacks were initiated in response to some visual trigger, such as larval movement. In cases where predation by adult yellow perch is found to be significant, it would be fruitful to determine whether larvae develop a behavioral refuge from predation by reducing their movement and feeding activity in the presence of adult yellow perch. This behavior would indicate a compromise between maximizing growth rate and minimizing mortality risk, which has been observed in adult and juvenile fish (Skalski and Gilliam 2002; Werner et al. 1983) but has not been reported for the larval stage. This finding merits further study, particularly in systems in which cannibalism is thought to be important.

Date of hatch distributions of larval survivors changed in the model in response to increases in size variability resulting from variation in mean growth rate. Low growth rates result in higher mortality and seem to favor larvae hatched later in the larval period, while higher growth rates result in lower overall mortality and no net survival benefit relative to DOH. This appears to result from late-hatch larvae being the smallest larvae in the system at the time when mortality is most size-dependent. Nonetheless, the survival pattern of a cohort with a high mean growth rate is still dependent on DOH as the survival advantage shifts from late-hatch to early-hatch individuals as the larval period progresses. These conclusions would be altered if growth rate and DOH were not independent in the model and this will be an important avenue of future model analysis. However, the key point is that even when size-dependent vulnerability to predation is due largely to changes in growth rate, mortality is still DOH-dependent and analysis of patterns in the DOH distribution will be informative regarding the effect of size-dependent predation on individual survival.

The relationship between growth rate variability and the intensity of size-dependent predation has been observed in previous individual-based model analyses (Pepin 1989; Rice et al. 1993; Cowan et al. 1996). However, these analyses did not include an examination of the resulting patterns in DOH distribution, which are informative for the comparison of model results to similar data from natural populations. Size-independent mortality, as well as size-dependent mortality acting on low size variability, favored survivors that hatched after peak hatch. In contrast, when size variability was increased by doubling the mean growth rate, the DOH distribution of survivors no longer favored later-hatched larvae.

One surprising result of the individual-based modeling analysis was that patterns in the characteristics of survivors did not change among the different predators tested in this experiment. Cowan and Houde (1992) found differences in

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predators to be an important factor in larval survival, but their study involved comparisons of predators across a wider taxonomic and behavioral range than our work. Similarity in effect of predation among predators in our experiments was likely due to the fact that encounters between large alewife (>160 mm TL) and small larvae (>7 mm TL) in the model were rare, and it was at the highest predator–prey size ratios (>20) that alewife capture efficiency and attack behavior deviated strongly from that of the other fish predators. At other size ratios, larval size is likely more important to individual vulnerability to predation than variance in size selectivity among these three fish predators.

When larvae were exposed to a predation pulse during the larval period, larval vulnerability to predation was highly dependent on DOH. Larvae that hatched in the 5–7 days preceding the predation period were expected to be more vulnerable to size-dependent predation by alewife than larvae hatched significantly before the predation period. As expected, larvae hatched during or preceding the predation window had lower survival than larvae born at other times, but the impact that this had on cohort survival and the DOH distribution of survivors depended on what portion of the cohort was affected. The lowest overall survival occurred when the predation window was near or immediately after peak hatch (days 11–15 or 16–20). The DOH distribution of survivors from this predation scenario also exhibited the highest survival advantage for later-hatched larvae and closely resembled a DOH pattern that was not size-dependent. As the predation window was placed successively later in the larval period, the non-selective signature (increased survival of later-hatched larvae), as well as the mortality rate, decreased. Just as in the growth rate variability experiment, high mortality is associated with a survival advantage for later-hatched larvae, and this advantage is reflected in the DOH distribution of survivors.

Our results suggest that not only is variance in DOH important to the full description of size variability, but it may provide a valuable detection tool for the selective signature left in characteristics of survivors of the larval stage. These subtle shifts in survival among different subcohorts can have dramatic effects on a subcohort's contribution to the year class, and IBM analysis can be a valuable tool for detecting even these relatively small shifts in the DOH distribution. In a similar model analysis of the timing of predation, Paradis et al. (1999) reported that a predation pulse during the early larval period favored smaller and presumably later-hatching individuals, but if the predator pulse occurred later in the larval period, then this pattern diminished. Their results support ours; however, detection of this pattern in larval size data from the field would be complicated by changes in growth rate among daily subcohorts. Rice et al. (1997) stated that size-selective mortality may be masked and difficult to detect in size data of survivors if reversals in selection occur during the life stage of interest. Date of hatch distributions would suffer from the same limitations, except they can be estimated at multiple points during the larval period and continually compared with the initial DOH distribution. Changes in the DOH distribution over the larval period observed in model simulations are also detectable in field data and may prove valuable for detecting size-selective mortality for a given cohort and making comparisons between cohorts. In this way, we can use the individual-based model as a tool for measuring the relative effects of sources of growth rate variation and sources of mortality on the DOH distribution of survivors. In turn, we can provide information on the importance of these factors to year-class strength based on how the DOH distributions resulting from model analysis match up to comparable field data. The utility of field data for identifying important sources of larval mortality has been questioned based on the differences in scale between traditional field sampling protocols and ecological effect (Pepin 1989, 2004). The combined use of field-collected data on larval DOH distributions and IBM analysis may provide a better tool set for elucidating the complex patterns of larval survival.

In general, size-selective predation on larval yellow perch in Lake Michigan may be weakly correlated with year-class strength at present because of low spatial overlap with predators at vulnerable sizes and densities. Size-selective predation is likely to play a stronger role in smaller systems that are more productive. Predation has been found to be important to year-class strength in other populations of yellow perch (Campell 1998; Mayer et al. 2001). Our conclusions regarding the current importance of predation in Lake Michigan represent an important difference between Lake Michigan and other systems.

An analysis of these differences is warranted before applying lessons learned from examination of perch populations in other systems to our understanding of population dynamics of yellow perch in Lake Michigan. In particular, differences in the importance of sources of mortality such as predation between yellow perch populations in Lake Michigan and yellow perch populations in other systems may be associated with differences in the size of the pelagic habitat; an increase in available habitat will affect local larval retention and the amount of overlap between predators and prey. The application of both field data analysis and individual-based models to the examination of characteristics of larval survivors is a valuable tool for detecting differences in patterns of size-dependent larval mortality. The individual-based model developed as a part of this analysis will be coupled with field data from systems in which predation is thought to be important to larval survival, such as Green Bay, in order to further improve our understanding of recruitment for larval yellow perch.

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Foraging selectivity by larval yellow perch (*Perca flavescens*): implications for understanding recruitment in small and large lakes

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Abstract: Growth and survivorship of larval yellow perch (*Perca flavescens*) have been examined in many systems but can conclusions from well-studied perch populations in smaller lakes be applied to populations in meso-oceanic systems like Lake Michigan, USA? Laboratory experiments were conducted with yellow perch (hatch to 35 mm total length) to develop an empirical selectivity function based on Chesson's α to describe larval diet as a function of changes in prey community composition. This function was used in an individual-based foraging and growth model (IBM) to describe changes in foraging decisions resulting from changes in prey composition between different systems. Larval perch made three selective transitions during ontogeny. Initial positive selection for rotifers and the relative selectivity for cladocerans vs. copepods in late-stage larvae were both dependent on prey composition. Larvae exposed to prey assemblages differing only in composition had different diets. The empirically based IBM accurately predicted these dietary differences and resulting differences in larval growth and likelihood of starvation between systems at equal prey density. The importance of feeding behavior to larval survival will differ between Lake Michigan and smaller lakes, and these results are important for comparisons of recruitment dynamics between large and small systems.

Résumé : La croissance et la survie des larves de la perchaude (*Perca flavescens*) ont été étudiées dans plusieurs systèmes, mais il reste à savoir si les conclusions tirées de populations bien analysées dans les lacs plus petits sont applicables aux populations de systèmes méso-océaniques, tels que le lac Michigan, É.-U. Nous avons mené des expériences de laboratoire avec des perchaudes (de l'éclosion à 35 mm de longueur totale) afin de mettre au point une fonction de sélectivité empirique basée sur l'α de Chesson pour décrire le régime alimentaire des larves en fonction des changements dans la communauté de proies. Cette fonction sert dans un modèle de la recherche de nourriture et de la croissance basé sur l'individu (IBM) à décrire les changements dans les décisions de recherche de nourriture résultant de variations de la composition des proies dans les divers systèmes. Les larves de perchaude traversent trois périodes de transition dans leur sélection alimentaire durant leur ontogénie. Une sélection initiale positive pour les rotifères et une sélection relative pour les cladocères par rapport aux copépodes chez les larves avancées sont toutes deux reliées à la composition des proies. Les larves exposées à des ensembles de proies qui diffèrent seulement par leur composition ont des régimes alimentaires différents. Dans des conditions de densité constante des proies, le modèle empirique IBM prédit de façon exacte ces différences de régime, ainsi que les différences qui en résultent dans la croissance larvaire et la probabilité de mourir de faim dans les divers systèmes. L'importance du comportement alimentaire pour la survie des larves diffère dans les petits lacs et dans le lac Michigan et ces résultats sont d'importance pour comparer la dynamique du recrutement dans des systèmes de grande et de petite taille.

[Traduit par la Rédaction]

Introduction

It is well-known that variability in mortality of larval fishes is often a significant factor driving variability in fishery recruitment (Sharp 1987). Mortality during the larval stage is affected by a variety of factors, including predation (Cowan and Houde 1993; Rice et al. 1993) and feeding success (Cushing 1990), and predicting larval mortality has proven elusive. In particular, interannual variation in survival of larval yellow perch (*Perca flavescens*) has been linked to pre-

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dation (Shroyer and McComish 2000), but the interaction of feeding success, growth, and survival has not been well described, particularly in larger systems.

Feeding success in fish larvae is affected by endogenous factors such as sensory ability (Blaxter 1986) and swimming performance (Webb and Weihs 1986; Fuiman et al. 1999) and by exogenous factors such as prey size and prey community composition (Kerfoot et al. 1980; DeVries et al. 1998). It is likely that larval fishes select prey based on a combination of these factors that is changing rapidly during ontogeny. Descriptions of larval diet based on endogenous factors only or on simplistic, exogenous models based only on prey size may fail to predict how changes in the prey community composition affect selection. Interactions of prey community structure with larval selectivity are particularly relevant for an analysis of feeding success of an opportunistic feeder such as larval yellow perch.

Yellow perch has a pelagic phase lasting 30–40 days that is generally associated with the ontogenetic period from hatch to the acquisition of juvenile characteristics, although the transition to demersal habitat generally occurs slightly later (Auer 1982). Yellow perch are widely distributed throughout North America in aquatic systems from 0.1 to 52 000 km^2 in area (Jenkins and Burkhead 1994). Such a wide range in habitat size suggests that perch may be exposed to a wide variety of foraging conditions throughout their distribution. Ontogenetic changes in taxonomic and size selectivity have been observed for larval perch within a variety of systems (surface area 0.1–392 km^2, mean depth 5–12 m; Bulkley et al. 1976; Mills et al. 1984; Wahl et al. 1993). In a comparative study of two lakes, Siefert (1972) found that yellow perch larvae in a shallow eutrophic lake (1.51 km^2, maximum depth 3.1 m) followed a typical selective pattern, first feeding on copepod nauplii, then on copepodites, and finally on the larger copepods and cladocerans; however, perch larvae in a deeper, oligotrophic lake (8.1 km^2, maximum depth 34 m) selected for rotifers at first feeding and never showed positive selection for cladocerans. Such observed differences in selective pattern for larval perch between systems suggest that larval yellow perch can respond to variance in prey composition by changing their feeding behavior independent of ontogenetic development. Such plasticity in feeding behavior may be important to comparisons of larval feeding, growth, and survival between systems that differ in prey community composition.

Yellow perch larval feeding has been studied in lakes of widely varying sizes (0.1–392 km^2), and prey community composition is not often cited as a potential cause of annual variation in survival for larval yellow perch within particular systems. Still, there are major differences between even the largest of these lakes and a more meso-oceanic system like Lake Michigan (52 000 km^2, mean depth 89 m), such as the rotifer- and copepod-dominated zooplankton community of Lake Michigan (Madenjian et al. 2002), and more spatial variation in the abundance of larger zooplankton (Fulford 2003). The significance of these differences for comparisons of yellow perch feeding and growth between Lake Michigan and other systems, and the corresponding implications for larval survival, are unknown.

We conducted a series of laboratory experiments to quantify larval selectivity as a function of both larval size and prey type using a broader range of natural prey choices than has been used in previous selection studies on larval yellow perch. We then used these data to develop an empirical function designed to describe the diet of larval yellow perch with minimal assumptions regarding optimality of prey. This function combined Chesson's alpha (α) as a measure of the larval preference and prey community composition from field data as a measure of prey availability to predict prey selection of individual larva. We used this function to build an individual-based foraging and growth model (IBM) uniquely suited to addressing how differences among prey communities may affect foraging selectivity and diet of larval yellow perch. We used this IBM to ask how larval prey selection and diet may change between Lake Michigan and a smaller regional system (Green Bay) and how these differences may translate to differences in larval growth rate and survival between systems.

Green Bay (4212 km^2, mean depth 20 m) is a shallow, productive embayment connected to Lake Michigan at the Lake's northwest corner and has been the focus of research into the growth and survival of larval yellow perch (Bremigan et al. 2003). Green Bay is generally considered to be a large system, but it is closer to the small end of the spectrum in comparison with Lake Michigan and has a zooplankton composition similar to that observed in smaller systems described above, where yellow perch feeding selectivity has been studied, such as Oneida Lake, New York (Hansen and Wahl 1981; Mills and Forney 1981), and Lake Mendota, Wisconsin (Schael et al. 1991). Comparisons of perch foraging dynamics between the main body of Lake Michigan and Green Bay should be very informative regarding differences in larval yellow perch foraging behavior between different sizes of systems. Further, Green Bay is located adjacent to Lake Michigan and is exposed to similar regional conditions. The proximity of the two systems offers an opportunity to address differences between systems resulting from differences in system size without the confounding effect of larger-scale factors such as climate or geography.

Methods

Selectivity experiments

A population (hereafter main population) of yellow perch larvae was established in the laboratory from egg skeins collected in Lake Michigan. Skeins were manually stripped from ripe females collected in gill nets about 1.2 km from shore at a depth of 10–20 m. Collected skeins were fertilized in the boat with milt from three to six males and returned to the lab for incubation. Hatching occurred within 12–14 days of fertilization, and larvae were maintained in the lab in a 2.4 m diameter tank at 15–18 °C under flow-through conditions. Larvae were initially fed a tank culture of rotifers and small zooplankton four to six times per day. Starting 5 days posthatch (dph), larvae were fed *Artemia* nauplii four times per day. At 10 dph, food changed again to a commercial pellet fed four times per day from automatic feeders.

Zooplankton prey for the experiments were collected from two sites: nearshore Lake Michigan and Lake Nagawicka (3.7 km^2, mean depth 11 m), which is located 40 miles (1 mile = 1.609 km) west of Milwaukee, Wisconsin. Zoo-

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plankton from nearshore Lake Michigan were collected 1.2 km from shore in waters 25 m deep by towing a 1 m diameter, 64 µm mesh plankton net in a circular pattern 2 m below the surface. Two 15 min tows were completed at each of two sites about 1 km apart along the same depth contour. Zooplankton from Lake Nagawicka were collected at a single site 0.5 km from shore in waters 20–30 m deep as described above, with the exception that net diameter and tow length were reduced to 0.5 m and 5 min, respectively. All zooplankton were returned to the lab and maintained under mild aeration.

Experimental trials were conducted in 2000 and 2001. The length range for larval yellow perch used in selectivity trials combined over both years was 5.5–35 mm total length (TL; 2–50 dph). In 2000, trials were conducted with three larval ages: 2 dph (mean length = 5.5 mm, standard deviation (SD) = 0.41 mm), 15 dph (8.6 mm, 0.91 mm), and 30 dph (12.3 mm, 1.4 mm). To begin each trial, 200 larvae were transferred from the main population to each of five 38 L aquaria and allowed to acclimate for 7 days. These larvae were maintained at 15–18 °C under flow-through conditions and were fed to satiation with live zooplankton collected from Lake Nagawicka for the first 5 days of the acclimation period. Feeding stopped on the sixth day of acclimation to ensure larvae would feed during the trial period and to allow pretrial zooplankton to be flushed from the system. Pretrial water samples indicated that no zooplankton remained in the trial tanks at the beginning of each trial period.

For this experiment, the objective was to present yellow perch larvae with as wide a range of prey choices as possible to assess larval selectivity under optimal conditions. Therefore, to begin a trial, Lake Nagawicka and nearshore Lake Michigan zooplankton were mixed equally and introduced into each trial tank at a target density of 250 organisms·L^{-1}. The number of zooplankton introduced into each tank was standardized based on zooplankton mass according to a predetermined mass–density relationship for mixed zooplankton (R. Fulford, unpublished data).

In 2001, trials were conducted at four larval ages: 15 dph (mean length = 7.9 mm, SD = 0.6 mm), 30 dph (11.6 mm, 1.3 mm), 40 dph (15 mm, 1.4 mm), and 50 dph (21.5 mm, 3.0 mm). Seven days prior to each trial date, larvae were moved from the main population to the trial tanks, and the acclimation process proceeded as described above for the 2000 trials. In 2001, we wished to measure larval selectivity changes in response to differences in the zooplankton community between nearshore Lake Michigan and an inland lake (Lake Nagawicka). Therefore the experimental system was expanded to 10 aquaria and two zooplankton treatments: nearshore Lake Michigan and Lake Nagawicka. Zooplankton from nearshore Lake Michigan and Lake Nagawicka were collected and maintained as described for the 2000 trials. For each trial, tanks containing acclimated larvae were randomly assigned to one zooplankton treatment or the other (nearshore Lake Michigan or Lake Nagawicka, $n = 5$ per treatment). Zooplankton were introduced into each tank at a target density of 250 organisms·L^{-1}. The number of zooplankton introduced into each tank was standardized based on zooplankton mass and a predetermined mass–density relationship established separately for each treatment.

In both years, larvae were allowed to feed for 30 min, and then they were removed from the tank, euthanized in tricaine methanesulfonate (MS-222), and preserved in 95% ethanol for stomach analysis. Zooplankton were sampled at the beginning and end of each 30 min feeding trial by lowering a 4 cm diameter polyvinyl chloride tube onto four randomly placed rubber stoppers on the bottom of each tank to collect four replicate 250 mL samples. Collected zooplankton were preserved in 95% ethanol for identification and enumeration. Data collected were used to calculate larval diet selectivity and the difference in zooplankton composition between treatments. Zooplankton samples collected at the end of each trial were also used to check resource depletion during the trial period. The objective was to keep resource depletion to less than 50% in any single trial. Maximum proportion of zooplankton consumed during any trial was 40% (mean proportion 22%).

Sample analysis

Mean total length on each trial day was calculated from length measured to the nearest 0.1 mm for 20 euthanized larvae from each trial tank. Stomach contents of preserved larvae ($n = 30$) were identified and enumerated by taxonomic group at 8× magnification. Taxonomic zooplankton groups were defined as rotifers, copepod nauplii, cyclopoid copepods, calanoid copepods, small cladocerans, and *Daphnia* spp. (Table 1). We chose to separate zooplankton into these groups based on consideration of differences in zooplankton size, morphology, and what is typically reported in the diet of larval yellow perch (Bulkley et al. 1976; Schael et al. 1991). The small cladoceran prey group was composed almost entirely of *Bosmina* spp. and *Eubosmina* spp. Lengths of whole prey items found in each stomach were measured to the nearest 0.1 mm with a digital imaging system (ImagePro 5.1, Media Cybernetics Inc., Silver Spring, Maryland).

Zooplankton in samples collected from each tank were also identified and enumerated by taxonomic group based on a complete count of samples ($n = 8$ per tank) from both the beginning and end of the trial period. Mean size of zooplankton from the tanks was measured to the nearest 0.1 mm for common taxa with a digital imaging system. Differences in zooplankton community composition among treatments were examined with a MANOVA (multivariate analysis of variance) comparison (SAS Institute Inc. 2002).

Diet selectivity

Larval selectivity was quantified with the Chesson's α statistic (Chesson 1983). Selectivity of larva k for prey type i is defined as

$$(1) \qquad \alpha_{i,k} = \frac{r_{i,k}/p_i}{\sum_{j=1}^{m} r_{j,k}/p_j}$$

where $r_{i,k}$ is the proportion of prey type i in the gut of larva k, and p_i is the proportion of prey type i in the experimental tanks for m different prey types. Lockwood (1998) recommended using proportional data rather than absolute number for each prey item in experiments where it is difficult to con-

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Table 1. Mean length and dry mass of the six larval prey types.

Prey item	Length (mm)	Intercept (a)	Exponent (b)	Mass (μg)	Reference
Rotifers	0.13	1.84	1.44	0.10	Dumont 1975
Copepods					
Nauplii	0.2	3.0	1.71	0.19	Culver et al. 1985
Calanoid	0.54	6.19	1.96	1.85	Culver et al. 1985
Cyclopoid	0.43	6.66	2.89	0.58	Culver et al. 1985
Small cladocerans[a]	0.3	17.74	2.22	1.2	Culver et al. 1985
Daphnia spp.	0.9	7.50	1.56	6.4	Culver et al. 1985

Note: Dry mass was calculated from mean length with relationships taken from the literature. Function used is mass = $a \times$ length^b.
[a]Small cladocerans were predominantly from the genus *Bosmina*; the length–mass function used is for *Bosmina longirostris*.

trol for variation in total consumption with a time-independent stopping rule.

Chesson's α is a useful metric of selectivity for modeling because it is numerically associated with a measure of attack and capture probability. Unlike some selectivity indices that have either a clear numerical or biological definition, Chesson's α has both and it can be used in the IBM to predict larval diet; this point will be expanded in a later section. Chesson's α was calculated for each individual fish (n = 30 per tank), and a mean of these values for each tank represented a replicate value of α for each treatment (n = 5 per treatment). For the analysis of selectivity patterns, selection was interpreted as neutral if the 95% confidence interval for α_i at a particular larval size included m^{-1} and either positive or negative if the 95% confidence interval was higher or lower than m^{-1}, respectively.

Zooplankton sampling

Data regarding the zooplankton community of Lake Michigan were obtained from samples collected every 3 days from June to August in 2000 and 2001. Sampling was conducted with triplicate vertical hauls of a 0.5 m diameter, 64 μm mesh plankton net at each of four sites between 1 and 5 km from shore. Samples were collected from the top 10 m of the water column at all sites. Zooplankton were preserved in 95% ethanol and returned to the lab for identification and enumeration of taxonomic groups (Table 1). Three 5 mL subsamples from each main sample were enumerated at 20× magnification in a counting wheel, and the combined count for all three subsamples was converted to density for each prey type based on a constant sample volume (sample depth × net mouth area).

Zooplankton community data for Green Bay were based on samples collected in 1998 and 1999. Samples were collected in a similar manner weekly in May and June at a site near Little Tail Point, Wisconsin (B. Belonger, unpublished data). The sampling period in Green Bay was earlier than in Lake Michigan because the larval period for yellow perch begins about a month earlier in Green Bay. Zooplankton were identified and enumerated as described for samples from Lake Michigan (J. Dettmers, unpublished data). Data from different years were used because comprehensive zooplankton data were not available for both systems in the same years. All zooplankton groups collected in zooplankton samples in Green Bay and Lake Michigan were present in collections used in laboratory experiments.

Individual-based foraging model

To examine the relationship between diet and growth for larval yellow perch, we adapted a general, larval fish, foraging IBM (Letcher et al. 1996) to predict growth and starvation rates of larval yellow perch from hatch to 45 dph (Fig. 1). This model predicted daily consumption of each prey type (Table 1) for each individual larva k based on larval length (l, mm) and a stochastic, sized-based encounter rate ($ER_{i,k}$), handling time ($HT_{i,k}$), and probability of attack and capture ($Q_{i,k}$). Encounter rate and handling time were calculated using the general model with parameters specific to larval yellow perch (Table 2); full details of these calculations can be found in Fulford (2003).

Probability of attack and capture for larva k on prey item i in a given day was calculated in the model with an empirical function based on the Chesson's α metric and derived from our size-based selectivity experiments (Fig. 1). The probability that the next prey item attacked and captured by larva k will be of prey type i ($Q_{i,k}$) has two components: (*i*) the selectivity of the larva defined empirically in our experiments and expressed as $\alpha_{i,k}$ and (*ii*) the relative abundance p_i of prey type i on a given model day.

The best-fit function between $\alpha_{i,k}$ and larval size (5–35 mm TL) was found separately for each prey type i based on a comparison of the least-squared fit to the data for a series of common functions. Function types tested were linear, logarithmic, exponential, second-order polynomial, generalized logistic, and double Weibull.

Chesson's α is generally insensitive to changes in prey relative abundance; however, selectivity will always be near zero for any prey type when its relative abundance falls below a threshold value (Chesson 1983). When relative density for a particular prey item falls below this threshold, negative selectivity for that prey item will be indicated because larvae did not encounter this rare prey type, not because of prey type avoidance. Therefore, a threshold was defined as the relative abundance below which selectivity was always negative because of an absence of that prey item in larval guts; trials for which relative abundance of any prey item was less than the threshold were not used to fit the larval size – selectivity relationship for that prey item.

The best function for each prey type was based on a coefficient of multiple determination (R_a^2) adjusted for the number of parameters in the model (Neter et al. 1990). The best-fit function for each prey type i was then used in the IBM to predict $\alpha_{i,k}$ for prey type i. Data used for calculations of $\alpha_{i,k}$ for larvae larger than 25 mm TL included diet and field zoo-

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Fig. 1. Flow chart summarizing the individual-based model for foraging and growth used for the numerical experiments. Starvation threshold was set at 53% of previous maximum dry mass for all model simulations.

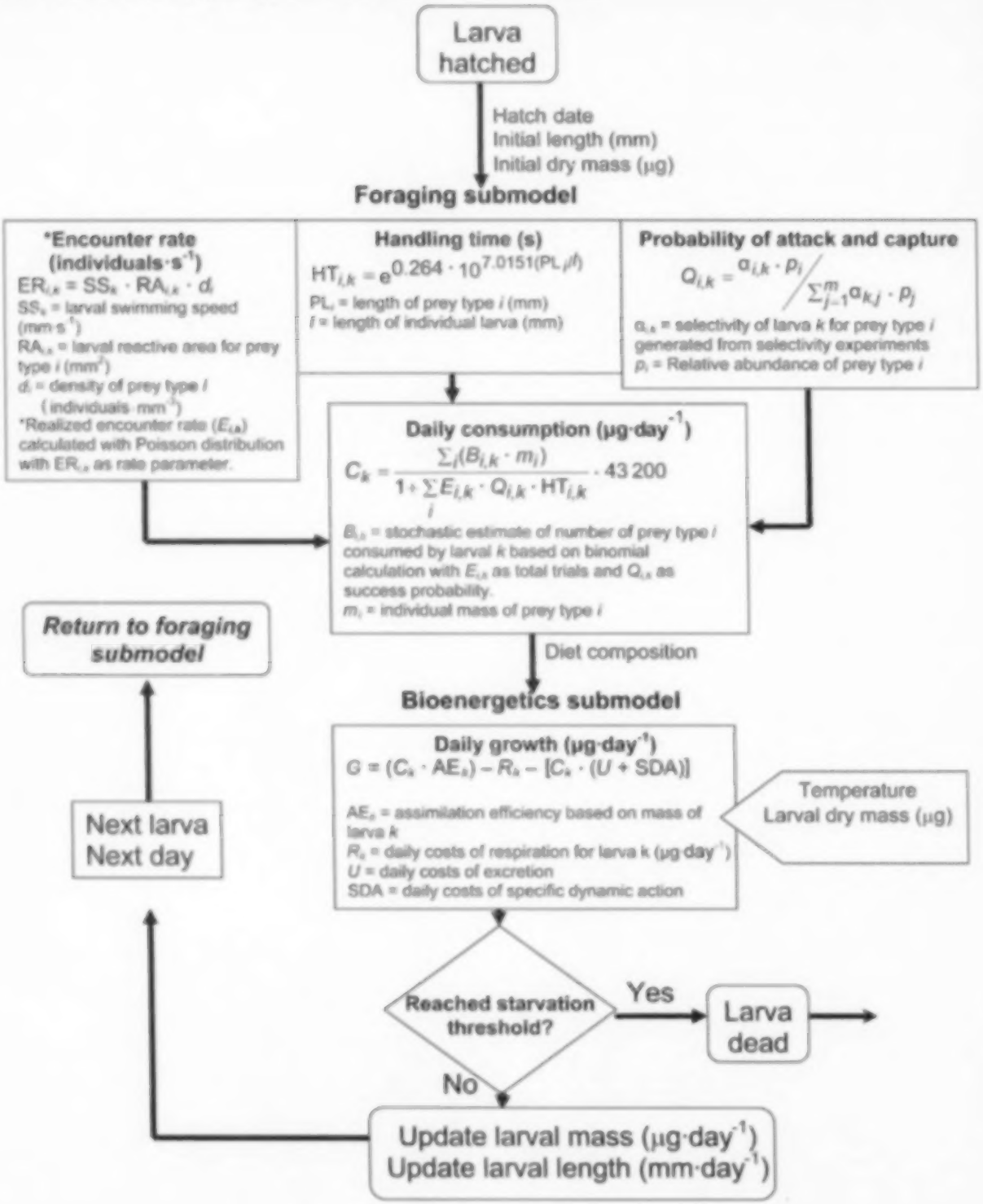
Larva hatched
Hatch date
Initial length (mm)
Initial dry mass (μg)
Foraging submodel
*Encounter rate (individuals·s⁻¹)
$ER_{i,k} = SS_k \cdot RA_{i,k} \cdot d_i$
SS_k = larval swimming speed (mm·s⁻¹)
$RA_{i,k}$ = larval reactive area for prey type i (mm²)
d_i = density of prey type i (individuals·mm⁻³)
*Realized encounter rate ($E_{i,k}$) calculated with Poisson distribution with $ER_{i,k}$ as rate parameter.
Handling time (s)
$HT_{i,k} = e^{0.264 \cdot 10^{7.0151(PL_i/l)}}$
PL_i = length of prey type i (mm)
l = length of individual larva (mm)
Probability of attack and capture
$Q_{i,k} = \alpha_{i,k} \cdot p_i \Big/ \sum_{j=1}^{m} \alpha_{k,j} \cdot p_j$
$\alpha_{i,k}$ = selectivity of larva k for prey type i generated from selectivity experiments
p_i = Relative abundance of prey type i
Daily consumption (μg·day⁻¹)
$C_k = \frac{\sum_i (B_{i,k} \cdot m_i)}{1 + \sum_i E_{i,k} \cdot Q_{i,k} \cdot HT_{i,k}} \cdot 43\,200$
$B_{i,k}$ = stochastic estimate of number of prey type i consumed by larval k based on binomial calculation with $E_{i,k}$ as total trials and $Q_{i,k}$ as success probability.
m_i = individual mass of prey type i
Return to foraging submodel
Diet composition
Bioenergetics submodel
Daily growth (μg·day⁻¹)
$G = (C_k \cdot AE_k) - R_k - [C_k \cdot (U + SDA)]$
AE_k = assimilation efficiency based on mass of larva k
R_k = daily costs of respiration for larva k (μg·day⁻¹)
U = daily costs of excretion
SDA = daily costs of specific dynamic action
Temperature
Larval dry mass (μg)
Next larva
Next day
Reached starvation threshold?
Yes
Larva dead
No
Update larval mass (μg·day⁻¹)
Update larval length (mm·day⁻¹)

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Table 2. Calculations used in the individual-based model (IBM) for larval swimming speed (SS, mm s^{-1}), larval reactive area (RA, mm^2), larval daily metabolic cost (R_k, µg day^{-1}), larval assimilation efficiency (AE), and larval dry mass-to-length conversion (W_k (µg) to length (mm)).

Model parameter	Submodel	Function	Source
Swimming speed	Foraging	Hatch 8 mm TL: 1 body length·s^{-1} >8 mm TL: 3 body lengths·s^{-1}	Houde 1969
Reactive area of larval k for prey type i	Foraging	$RA_{i,k} = \left[\frac{PL_i}{2\tan(\alpha_k/2)}\right]^2 \pi \cdot 0.5$	Letcher et al. 1996
Daily metabolic cost	Bioenergetics	$R_k = W_k \cdot 0.0065 \cdot W_k^{-0.2} \cdot f(t) \cdot 4.4$	Hanson 1997
Assimilation efficiency	Bioenergetics	$AE_k = 0.8(1 - 0.25\,e^{-0.0002(W_k - 600)})$	Letcher et al. 1996
Length – dry mass relationship	Initial inputs Bioenergetics	$W_k = 0.519\ \text{length}^{3.201}$	Mills and Forney 1981; C. Heyer[a], T. Miller[b], and B. Letcher[c], unpublished data

Note: Larval length is total length (TL) and Hatch refers to total length at time of hatching. PL_i, length (mm) of prey type i; α_k, angle (radians) of visual acuity for a larva of length k; $f(t)$, relationship between water temperature (t, °C) and daily metabolic cost. The function $f(t)$ and the formula for α_k are defined in Fulford (2003).

[a]Maryland Department of Natural Resources, Annapolis, MD 21401.
[b]University of Maryland Center for Environmental Science, Solomons, MD 20688.
[c]Conte Anadromous Fish Research Center, USGS/BRD, Turner Falls, MA 01376.

plankton data from the literature (Bulkley et al. 1976; Mills et al. 1984). Diet selectivity indices were calculated for yellow perch in these studies, but in cases where the index was not Chesson's α, we converted the selectivity index to Chesson's α. In the model, $Q_{i,k}$ is calculated each day for each larva k and each available prey item i.

The number of each prey type consumed in a given day was then converted to mass (µg dry mass) by multiplying the number of each prey type i eaten in a day by the mean mass of prey type i. Mean mass for each prey type was derived from a prey type specific, length–mass relationship and mean length for each prey type taken from zooplankton collected in Lake Michigan (Table 1). Zooplankton relative abundance in the model was based on the average seasonal pattern observed during the yellow perch larval period over 2 years for each prey type taken from the field data for either Green Bay or Lake Michigan. Zooplankton density was manipulated as a part of the numerical experiments (described below).

Individual-based bioenergetics model

Total mass consumed by larva k each day was converted to individual daily growth (µg dry mass) in a bioenergetics submodel adapted from two models: one developed previously for larval yellow perch (Hanson 1997) and a general larval bioenergetics model developed specifically for an IBM approach (Letcher et al. 1996). The combined model uses a mass-balance approach to predict daily growth (G, µg·day^{-1}) from predicted daily consumption (C, µg·day^{-1}) from the foraging submodel (Fig. 1). Larval mass was updated daily based on predicted growth. During a model run, a larva could not lose length but could lose mass based on the difference between total daily consumption predicted by the foraging submodel and calculated daily metabolic costs. If a larva lost more than 53% of its previous maximum mass at any point in a model run, then that larva starved to death. If larval mass increased beyond the previous maximum value for larva k, length was updated based on a length–mass conversion (Table 2). Full details regarding the bioenergetics model used are available in Fulford (2003).

Input to the bioenergetics submodel was daily mean water temperature and current dry mass of larva k. Daily mean temperature data were taken from a variety of sources depending on the system being modeled. Temperature data for nearshore Lake Michigan were taken from hourly temperature records collected 1 m below the surface at a site located 1.2 km from shore due east of Texas Rock near Milwaukee, Wisconsin (42°59′60″N, 87°50′38″W), from June to August 1999–2001 (R. Fulford, unpublished data). Temperature data for Green Bay were taken from temperature data collected hourly at the surface of the intake canal for the Pulliam power plant in Green Bay, Wisconsin, and from weekly temperature measurements taken at the surface 0.5 km from shore near Little Tail Point on the southwestern side of Green Bay. Little Tail Point is located 15 km north of the City of Green Bay. The area around Little Tail Point is a known spawning area for yellow perch (B. Belonger, unpublished data).

Each model simulation began with 1000 larvae, and initial size was randomly assigned to each larva from a normal distribution (mean = 5.7 mm, SD = 0.3 mm). Initial mass was calculated from randomly assigned length according to a larval yellow perch specific mass–length formula (Table 2). Model output was larval size-specific diet data, individual and cohort mean growth rate over the period from hatch to 45 days, distribution of size at age for the entire cohort, and the proportion of larvae that starved to death during each model run.

Numerical experiments

We conducted two numerical experiments with the foraging and growth IBM to address two questions. First, we wanted to establish that the model would accurately predict diet for larvae exposed to different prey assemblages. To accomplish this, the functions relating $\alpha_{i,k}$ to larval TL were fit to a subset of the data from selectivity trials (n = 45 tri-

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als). We then used the model to predict the diet of larvae exposed to the prey assemblage in the remaining set of reference data (n = 10 trials). The reference data were for larvae between 7 and 15 mm TL and were broken into two sets: larvae exposed to a zooplankton community from nearshore Lake Michigan and larvae exposed to a zooplankton community from Lake Nagawicka. These predictions were then compared with a χ^2 analysis to observed diet for larvae used in the reference trials.

Second, we asked how larval growth rate, size at age, and likelihood of starvation are affected by differences in zooplankton community composition between Green Bay and Lake Michigan. The model was run with two separate prey assemblages consisting of zooplankton composition observed in nearshore Lake Michigan in 2000–2001 or in Green Bay in 1998–1999. Simulations were conducted at 50, 100, 150, 200, and 250 prey·L^{-1} for each zooplankton assemblage. A broad range of zooplankton densities was used to explore more generally relevant patterns in growth and survival as a function of prey density than observed in just the 2 years for which we had data. We also wanted to explore more directly how the interacting effects of prey density and composition on larval growth and starvation mortality differ between nearshore Lake Michigan and Green Bay. The range of zooplankton density used in this experiment approximates the full range of daily and site-specific mean zooplankton densities observed in both nearshore Lake Michigan and Green Bay (Fulford 2003; J. Dettmers, unpublished data). Three replicate model runs were conducted for each combination of zooplankton density and zooplankton assemblage to account for variability due to stochastic functions in the model.

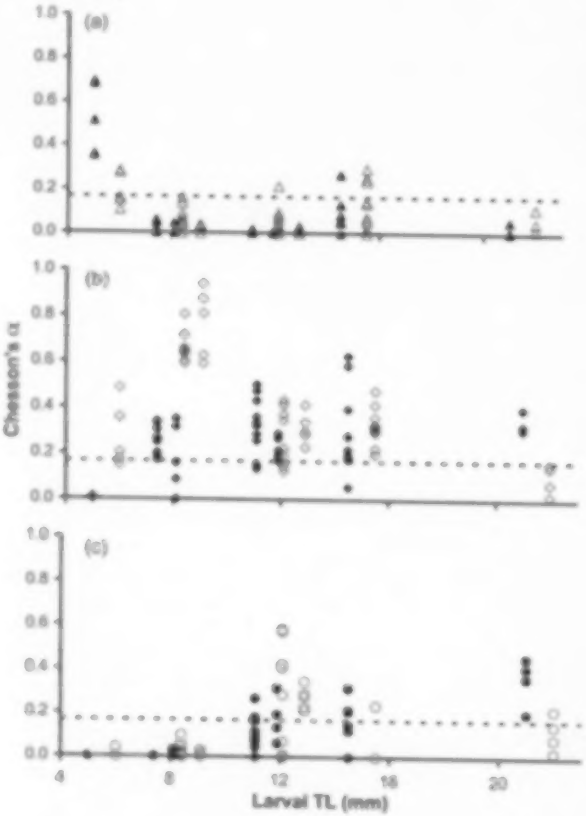
Results

Selectivity experiments

The three zooplankton assemblages used in selectivity trials (nearshore Lake Michigan, Lake Nagawicka, and mixed) differed significantly in composition (Wilks' λ, $F_{[12,94]}$ = 12.34, $p < 0.0001$). The Lake Michigan treatment was dominated (>70%) by rotifers, while the Lake Nagawicka assemblage was composed largely of *Daphnia* spp. and cyclopoid copepods. The mixed assemblage was the most balanced among prey types but remained high in rotifers (>40%). Mean initial zooplankton density in the trials tanks was 382 prey·L^{-1} and ranged from 112 to 782 prey·L^{-1}. The higher than expected mean and variance in zooplankton density in the tanks was due largely to variance in rotifer density, because rotifers can vary in number without having much affect on total mass of a zooplankton sample. However, high zooplankton density in the tanks should not bias our measurements of selectivity as long as density is high enough to generate larval feeding activity.

Values of α for rotifers indicated strong positive selection by 5.5 mm larvae, but dropped quickly to near zero, indicating negative selection at all larger larval sizes (Fig. 2*a*). Values of α for copepod nauplii were also highest for larvae at 5.5 mm TL, but selection was neutral rather than positive. Selection for nauplii was generally neutral up to 15 mm TL, and α values showed no trend with size (Fig. 2*a*).

Fig. 2. Chesson's α for larval yellow perch (*Perca flavescens*) feeding on m = 6 prey types: (*a*) rotifers (▲) and copepod nauplii (△), (*b*) calanoid (◆) and cyclopoid copepods (◇), and (*c*) small cladocerans (●) and *Daphnia* spp. (○). The horizontal broken line represents no selection and is set at m^{-1}. Symbols are offset by +0.5 (open) or –0.5 (solid) on the x axis for clarity. TL, total length.



Selection differed for cyclopoid and calanoid copepods (Fig. 2*b*). Values of α for cyclopoid copepods were initially neutral but rose sharply for larvae at 8 mm TL, indicating a period of strong positive selection by early-feeding larvae. Larval selection for cyclopoid copepods was neutral for larvae larger than 12 mm TL. Data from the literature used in the model also suggest that selectivity for cyclopoid copepods by yellow perch larvae at 26.5 mm TL is neutral (Bulkley et al. 1976).

Selection for calanoid copepods was negative for yellow perch larvae at 5.5 mm TL. Values of α rose with larval size beginning around 8 mm TL and were generally positive for larvae larger than 12 mm TL (Fig. 2*b*). Data from the literature used in the model suggest that selection for calanoid copepods by larvae at 26.5 and 35 mm TL is consistently positive (Bulkley et al. 1976; Mills et al. 1984).

Selectivity patterns for cladocerans all showed similar patterns with slightly different shapes (Fig. 2*c*). Selectivity for small cladocerans was negative for all larvae less than 12 mm TL, became neutral for larvae between 12 and

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Table 3. Summary of the model fit between Chesson's α and larval total length (L, mm) for each prey type based on experimental data.

Prey Item	Model type	Parameters	R^2
Rotifers	Power: $\alpha = a L^b$	a = 193 499	0.89
		b = –7.64	
Copepods			
Nauplii	No trend	Mean α = 0.07	NA
Cyclopoid	Polynomial: $\alpha = a_1 L^2 + a_2 L + a_3$	a_1 = –0.042	0.67
		a_2 = 0.75	
		a_3 = –2.60	
Calanoid	Log-linear: $\alpha = a \ln(L) + b$	a = 0.272	0.68
		b = –0.3834	
Small cladocerans	Logistic: $\alpha = \frac{a_1}{\left[1 + \left(\frac{a_1}{a_2} - 1\right) e^{-a_3 a_4 L}\right]^{1/a_4}}$	a_1 = 0.40	0.65
		a_2 = 0.09	
		a_3 = 13	
		a_4 = 0.031	
Daphnia spp.	Logistic: $\alpha = \frac{a_1}{\left[1 + \left(\frac{a_1}{a_2} - 1\right) e^{-a_3 a_4 L}\right]^{1/a_4}}$	a_1 = 0.445	0.86
		a_2 = 0.092	
		a_3 = 20	
		a_4 = 0.029	

Note: Larval size range was 5.5–35 mm total length for all functions, and data for larvae >25 mm total length includes data from the literature.

15 mm TL, and was positive for larvae greater than 21.5 mm TL. Data from the literature (Bulkley et al. 1976) suggest that values of α for larvae between 26 and 35 mm TL are above m^{-1}, indicating that selection for small cladocerans by yellow perch larvae larger than 21.5 mm is consistently positive.

Larval selectivity for *Daphnia* spp. was negative for larvae at 5.5 and 8 mm TL, but neutral or positive at 11.6 and 12.2 mm TL (Fig. 2*c*). Values of α for larger larvae did not rise above m^{-1} in this experiment, but mean relative density of *Daphnia* spp. only ranged from 0.01% to 0.03% in replicate tanks at all larger larval sizes tested. These low density values suggest that negative selection in these trials for *Daphnia* spp. was due to low encounter rates rather than larval preference. Selectivity data from the literature used in the model for larvae at 26.5 and 35 mm TL suggest positive selection for *Daphnia* spp. by larger larval yellow perch (Mills et al. 1984; Schael et al. 1991).

Parameterizing the IBM

Based on the selectivity data, the relative abundance minimum threshold for inclusion in the function was set at 0.03%. When relative abundance of a particular prey item in a trial was below 0.03% of the assemblage, data from that trial were not used to fit the larval size – selectivity relationship for that prey item.

No single function fit the data relating Chesson's α to larval TL best for all six prey types (Table 3). Selectivity for rotifers was best described by a power function (Fig. 3*a*). The model fit was highest for rotifers among all prey types. We observed no relationship between larval selectivity for copepod nauplii and larval size; selectivity for nauplii in the model was described with the mean value of α for nauplii across all larval sizes (0.07; Fig. 3*b*). Selectivity for cyclopoid copepods was best described by a second-order polynomial function with a minimum α level set at m^{-1} (Fig. 3*c*). This function allowed for the steep rise in α for larvae around 8 mm TL and predicted neutral selection for larvae larger than 12 mm TL. Selectivity for calanoid copepods was best described by a logarithmic regression, with a maximum α value of 0.4 for larvae larger than 15 mm TL (Fig. 3*d*). Selectivity for both small cladocerans and *Daphnia* spp. was best described by a generalized logistic function (Figs. 3*e*, 3*f*). Values of α for both cladoceran groups were low initially and rose with increasing larval size.

Zooplankton community composition

The nearshore Lake Michigan zooplankton assemblage was dominated numerically by rotifers (80%; Fig. 4*a*). Prey densities across sites in nearshore Lake Michigan in 2000–2001 were between 50 and 200 prey·L^{-1}, with a 2-year mean density of 75 prey·L^{-1}. In contrast, the prey assemblage of Green Bay was more diverse. Cladocerans and copepods were nearly equal in abundance, and no prey type represented more than 50% of the total assemblage at any time over the larval period (Fig. 4*b*). Prey densities in 1998–1999 in Green Bay were between 50 and 300 prey·L^{-1}, with a 2-year mean density of 124 prey·L^{-1} over both years.

Numerical experiments

In experiment one, model predictions of diet for larvae feeding on a nearshore Lake Michigan or Lake Nagawicka zooplankton assemblage did not differ significantly from observed diet (χ^2 = 1.23, degrees of freedom (df) = 5, $p > 0.1$), which suggests the model performed well (Fig. 5). Diets for larvae exposed to the nearshore Lake Michigan assemblage were dominated by calanoid and cyclopoid copepods, with rotifers and cladocerans being a minor dietary component. In

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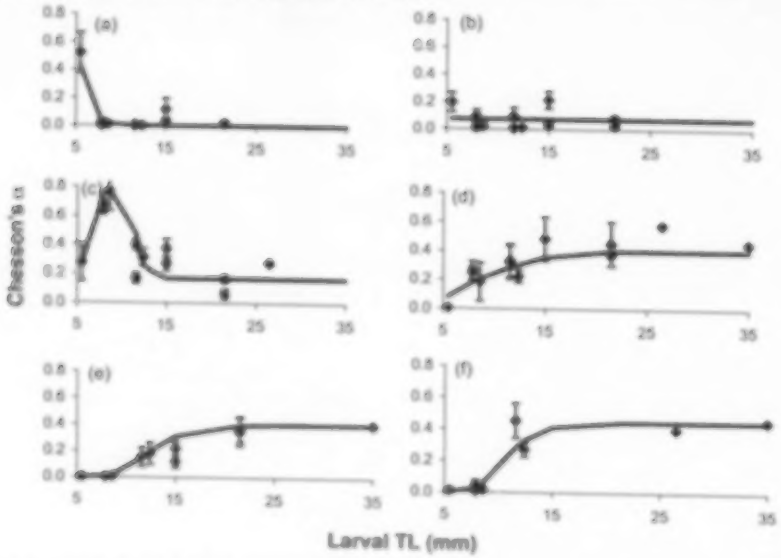
Fig. 5. Chesson's α data (◆) and best model fit to the data for a prey type specific function (solid line) relating Chesson's α to larval total length (TL, mm) for (*a*) rotifers, (*b*) copepod nauplii, (*c*) cyclopoid copepods, (*d*) calanoid copepods, (*e*) small cladocerans, and (*f*) *Daphnia* spp. as prey. Error bars for data are 95% confidence intervals.



contrast, diets of larvae exposed to the Lake Nagawicka assemblage were composed mostly of *Daphnia* spp., with calanoid copepods a distant second in relative dietary abundance. There were noticeable differences between what was available to and what was eaten by larvae, particularly for the nearshore Lake Michigan treatment, where larvae avoided rotifers despite their high relative abundance. However, available prey composition did not differ significantly from either observed diet or model predictions ($\chi^2 = 1.3$, df = 5, $p > 0.1$).

In experiment two, larvae exposed to the nearshore Lake Michigan assemblage in the model fed mainly on rotifers and copepods initially and made a transition to mainly larger calanoid copepods as they grew, mainly at the expense of rotifers (Fig. 6*a*). Larvae exposed to the Green Bay assemblage in the model fed largely on cyclopoid copepods initially, avoided the smaller rotifers, and shifted gradually to a diet split between small cladocerans and *Daphnia* spp. as they increased in size. The transition to small cladocerans and *Daphnia* spp. was predicted to occur around 20 mm TL, and these two items dominated larval diet in Green Bay for the remainder of the model run (Fig. 6*b*).

These observed differences in diet between larvae exposed to different prey assemblages translated into differences in both growth and survivorship in the model. Larvae allowed to forage on the Green Bay assemblage had a higher predicted mean growth rate compared with nearshore Lake Michigan larvae at all prey densities except the lowest (50 prey·L^{-1}). Growth rates for larvae exposed to the nearshore Lake Michigan assemblage did not rise substantially until prey density rose above 100 prey·L^{-1} (Fig. 7). Growth rates for larvae exposed to the Green Bay prey assemblage were also low at a density of 50 prey·L^{-1} but rose more rapidly between 50 and 200 prey·L^{-1}. Further, more than 50% of simulated larvae exposed to the nearshore Lake Michigan assemblage starved at prey densities fewer than 150 prey·L^{-1} (Fig. 8). Starvation rates for larvae exposed to the nearshore Lake Michigan assemblage declined linearly with increasing prey density over the entire density range (50–250 prey·L^{-1}). In contrast, larvae exposed to the Green Bay assemblage had a high starvation rate at the lowest density, but it dropped rapidly to around 20% or lower for prey densities at or above 150 prey·L^{-1} (Fig. 8).

These differences in growth and survivorship were reflected in larval size distributions at the end of the model runs. Larval survivors that fed on the Green Bay prey assemblage (Figs. 9*b*, 9*d*) had a wider size range and were generally larger than larval survivors that fed on the nearshore Lake Michigan assemblage (Figs. 9*a*, 9*c*) at the same prey density. At a prey density of 250 prey·L^{-1}, both distributions were bimodal, but the major mode in the length distribution for larvae exposed to the Green Bay assemblage (mode centered on 34 mm TL) included most of the larval survivors. The minor mode in the length distribution of the Green Bay assemblage (at ~20 mm TL) overlapped the major mode in the length distribution of the nearshore Lake Michigan assemblage (at ~18 mm TL). The minor mode in the length distribution of larval survivors exposed to the nearshore Lake Michigan assemblage (7 mm TL) was composed of larvae demonstrating little or no growth over the model period. In contrast, the minor mode of larvae exposed to the Green Bay assemblage was composed of larvae that grew substantially.

The size distribution of larval survivors exposed to both prey assemblages at a lower mean density (100 prey·L^{-1}) had similar length ranges as observed at the higher prey density, but the peak in larval size dropped 5 and 13 mm for larval exposed to the nearshore Lake Michigan and Green Bay assemblages, respectively (Figs. 9*a*, 9*b*). In the case of larvae exposed to the nearshore Lake Michigan assemblage, the

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Fig. 4. Relative abundance of six prey types in field samples collected during the pelagic larval period for yellow perch (*Perca flavescens*) in (*a*) nearshore Lake Michigan and (*b*) Green Bay. From the bottom of each panel to the top, the prey items are rotifers, nauplii, calanoids, cyclopoids, small cladocerans, and *Daphnia* spp.

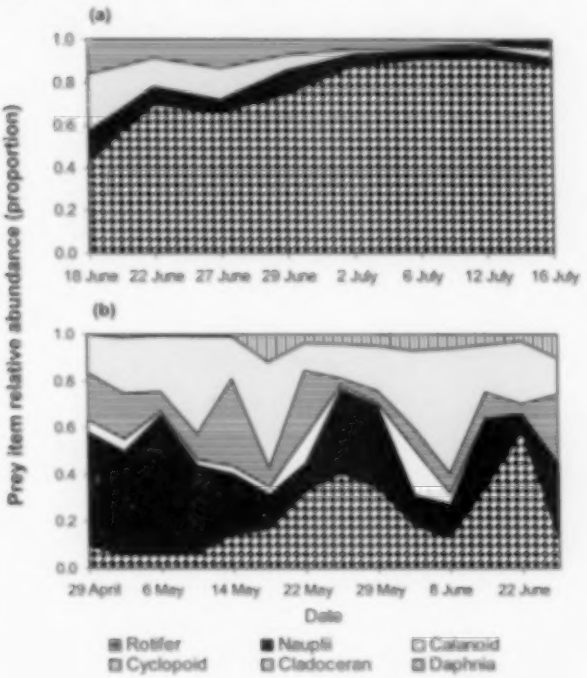
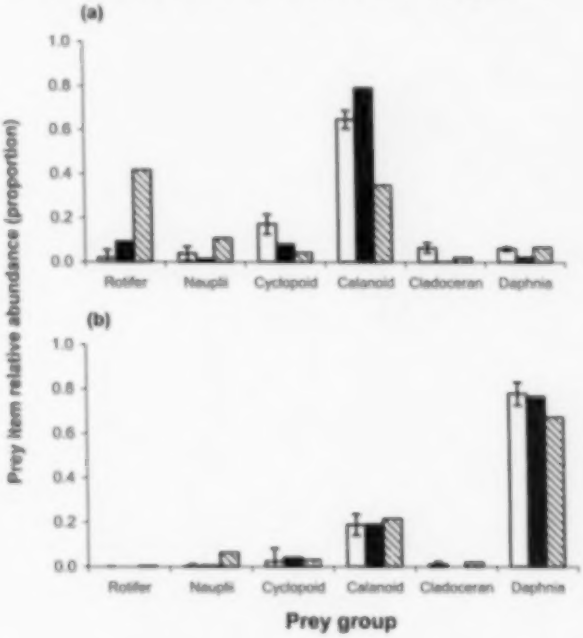


Fig. 5. Comparison of observed diet (±1 standard error; open bars), diet predicted by our individual-based foraging model (solid bars), and prey availability (hatched bars) for larval yellow perch (*Perca flavescens*; 7–15 mm total length) exposed to a prey assemblage from either (*a*) nearshore Lake Michigan or (*b*) Lake Nagawicka.



distribution was no longer bimodal, as observed in this distribution at the higher prey density.

Discussion

Diet shifts and community composition

Larval yellow perch appear to make three distinct transitions in selection throughout ontogeny: from rotifers to small copepods to large copepods and cladocerans. However, the first and last transitions seem most dependent on prey community composition.

Larval yellow perch initially showed positive selection for rotifers in our selectivity experiments. This early preference for rotifers has been observed in field data from other oligotrophic systems (Siefert 1972). Surprisingly, a preference for rotifers appears to lower predictions of larval survival. Larvae that switched to small copepods at a smaller size in the model had a distinct growth advantage over larvae that fed largely on rotifers, but this energetic conclusion does not appear to translate to a high preference for copepods in early-stage larvae. Low or negative growth for yellow perch larvae that have been fed rotifers has been observed previously in laboratory experiments (Graeb et al. 2004).

It could be that first-feeding larval yellow perch select rotifers simply because they are much more abundant and easy to catch and that this initial positive selection is dependent on limited foraging ability rather than true preference. The full recruitment of visual acuity occurs after first feeding in larval yellow perch (Wahl et al. 1993); first-feeding larvae are likely to select prey based on a more immediate definition of optimality (i.e., avoiding starvation). Model results do predict that larvae exposed to the Green Bay prey community (i.e., low rotifer abundance) will switch to small copepods earlier than larvae exposed to a nearshore Lake Michigan prey community (i.e., high rotifer abundance), and early-stage larvae feeding on copepods have a major growth advantage over larvae that are not. Such selective choices demonstrate the difference between the long- and short-term optimality of foraging decisions. In the short term, it is clearly optimal to eat rotifers rather than nothing at all. However, in the long term, larvae that shift to higher value prey will grow faster and are more likely to survive the larval stage. Model predictions suggest that larvae that fail to make this early transition may be trading a death from starvation for a death by size-selective processes (i.e., predation) and are no more likely to contribute to the year class than larvae that eat nothing at all.

The final transition in larval diet prior to the beginning of the juvenile stage involves a community-dependent trade-off between larger copepods and cladocerans. Larval perch were predicted to select for cladocerans at intermediate larval sizes even when cladocerans comprised only 1% of the prey assemblage. However, the nearshore Lake Michigan prey assemblage frequently had less than half a percent cladocerans in 2000–2001, and larvae exposed to this prey community in

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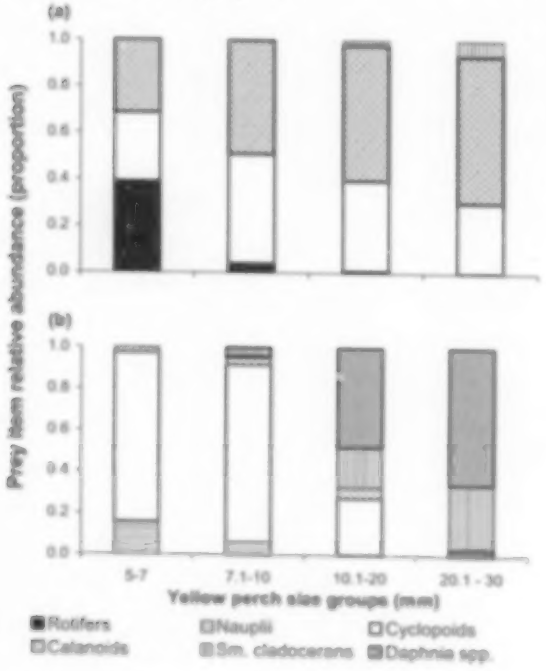
Fig. 6. Mean diet composition for larval yellow perch (*Perca flavescens*) from model runs (N = 3, 1000 larvae per run) exposing larvae to a zooplankton assemblage from either (*a*) nearshore Lake Michigan or (*b*) Green Bay. From the bottom of each panel to the top, the prey items are rotifers, nauplii, calanoids, cyclopoids, small cladocerans, and *Daphnia* spp. Not all prey items are visible in a single panel.



the model shifted their selection to larger calanoid copepods. Larval yellow perch larger than 16 mm TL showed positive selection for calanoid copepods in all assemblages, but the importance of calanoids tended to vary based on the relative abundance of cladocerans.

Laboratory experiments have demonstrated that late-stage larval perch positively select for calanoid copepods and incur a growth advantage by doing so (Confer and Lake 1987). Nevertheless, positive selection for cladocerans has been consistently observed for yellow perch larvae in field data from other systems, including Lake Mendota (Schael et al. 1991) and Oneida Lake (Hansen and Wahl 1981; Mills et al. 1984), but the timing of this transition with respect to larval size varies greatly. Variance in the observed onset of positive selection for *Daphnia* spp. may be due in part to variance in the composition of the *Daphnia* complex between systems. *Daphnia* spp. collected in Green Bay, Lake Nagawicka, and nearshore Lake Michigan were mainly medium-bodied *Daphnia* spp. (0.62–1.17 mm). In contrast, Oneida Lake is dominated by *Daphnia pulex*, which has a size range of 0.7–2.1 mm (Mills et al. 1984). Positive preference for *Daphnia* spp. was evident at a smaller larval size in our data compared with similar data from other systems; this difference is most likely due to observed differences in the size of the *Daphnia* complex. Such differences are an important reason

Fig. 7. Mean growth rate from model runs comparing larvae exposed to a zooplankton assemblage from nearshore Lake Michigan (●) or Green Bay (△) over a range of zooplankton densities. N = 1000 larvae per model run.

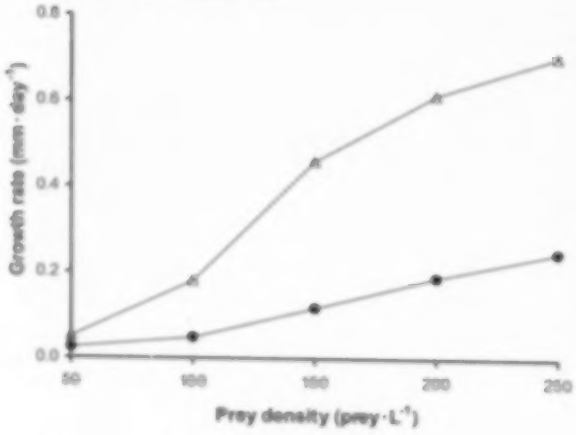
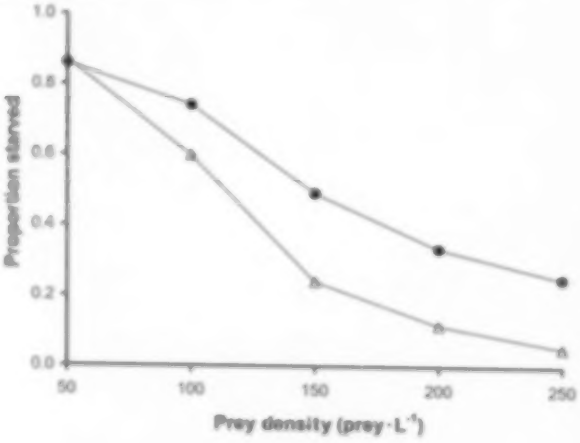


Fig. 8. Proportion of larvae that starved to death per model run (N = 1000) for larvae exposed to a zooplankton assemblage from nearshore Lake Michigan (●) or Green Bay (△) over a range of prey densities.



to understand both size and taxonomic selectivity for larval perch.

Predicting larval diet shifts

Our empirical approach to predicting larval diet is well suited to understanding larval responses to changing prey community composition. Traditional approaches to modeling larval foraging have used optimization rules, such as maximization of the benefit–cost ratio (Eggers 1977). This approach has two distinct disadvantages for comparing feeding selectivity between different prey assemblages. First, optimization rules are frequently based on inherent qualities of prey, and decisions regarding prey type i do not directly take into account the relative abundance of all available prey types. As a result, changes in diet composition in optimality models often occur abruptly when prey density crosses a dis-

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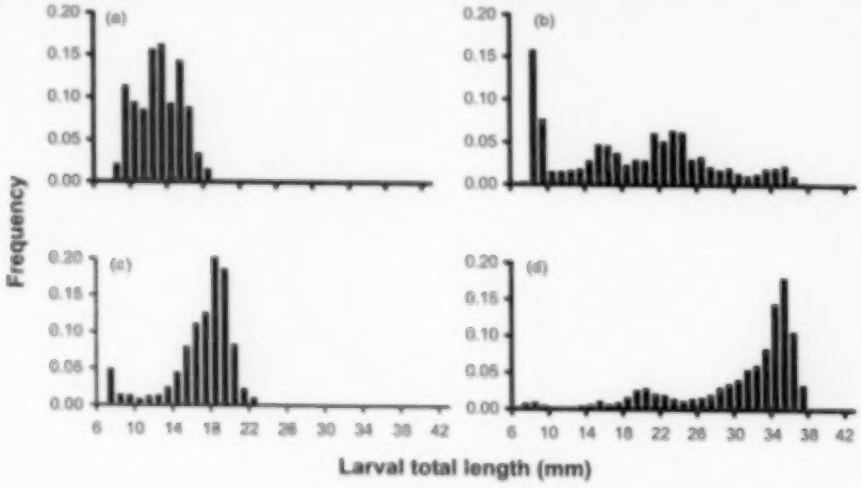
Fig. 9. Size–frequency distribution of predicted larval survivors at 30 days after peak hatch based on model simulations ($N = 3$, 1000 larvae per run) at (*a*, *b*) 100 prey·L^{-1} and (*c*, *d*) 250 prey·L^{-1}. Larvae were exposed to a prey assemblage from either (*a*, *c*) nearshore Lake Michigan or (*b*, *d*) Green Bay.



crete threshold. Such changes result in prey types being included or not included in the diet in a "knife-edge" fashion not representative of the real world (Stephens and Krebs 1986). Such optimization-based models are not well suited to predicting gradual shifts in selection, such as shifts caused by subtle changes in prey relative abundance.

A second disadvantage of optimization rules is that they require an assumption regarding what criteria would be of value to the larva to rank prey types. This criterion is usually size, as this is the most numerically and biologically tenable metric available (Eggers 1977). Prey frequently differ in other significant ways, such as behavior and morphology (Kerfoot et al. 1980), which are more difficult to quantify.

Our empirical approach to predicting prey selection for larval yellow perch allows for selection without assumptions regarding optimal criteria. That is, size is considered as a criterion for selection just as it is in an optimality model, but it is bundled with other less mathematically tenable characteristics of prey that may also be important. This approach exploits a selectivity metric (Chesson's α) that describes changes in larval preference, is mathematically tenable, and is resistant to most changes in the prey assemblage. There is a minimum relative abundance greater than zero, below which selectivity data are affected, but it was extremely low in this study (0.03%) and is only likely to be important for extremely simple prey communities (Confer and Moore 1987). By utilizing empirical data, we were able to more accurately describe how selection for a particular prey item may change both as a function of larval size and as larvae are exposed to different prey assemblages.

Two potential sources of bias exist in this empirical approach to measuring larval selectivity. First, a significant amount of variation among prey may exist within the taxonomic prey types. We have tried to define prey types in our model so that this bias is minimized. It does appear that variation among species of *Daphnia* may be important. The onset of positive selection for *Daphnia* spp. occurred relatively early in our selectivity trials compared with observations of yellow perch in smaller systems, likely because of differences in the size of the dominant *Daphnia* species between systems like Oneida Lake and Lake Michigan. Differences within the *Daphnia* species complex would need to be addressed to increase the generality of model results. These differences strengthen the argument that comparisons of selectivity data for larval yellow perch between systems warrant greater scrutiny.

A second potential source of bias in this analysis is differential digestion of hard- vs. soft-bodied zooplankton in larval guts (Sutela and Huusko 2000). Smaller, softer-bodied prey such as rotifers would be less likely to be present in the gut, so selection for these prey types might be underestimated. By limiting the foraging experiments to half an hour, we likely minimized the impact of this bias in comparison with analysis of field-collected larvae, for which total digestion time is unknown. Our results generally agree with recent field-based results on larval yellow perch diet in Green Bay (Bremigan et al. 2003); however, digestive bias may also be a reason why rotifers are not often cited as an important item in larval guts from field data.

Data from the literature suggest that larvae of comparable size in different systems can make very different foraging decisions. For instance, larval perch in Clear Lake, Iowa, fed primarily on copepods up to a larval size of 25 mm TL (Bulkley et al. 1976), but larvae of similar size in Oneida Lake, New York, showed a strong positive selection for *Daphnia* spp. (Mills et al. 1984). Similar studies on larval and juvenile European perch (*Perca fluviatilis*) have shown variance in selectivity for cladocerans vs. copepods among systems ranging from small lakes to coastal embayments, which suggests that variable selection based on prey community composition is a trait these two species share (Persson and Greenberg 1990; Mehner 2000). Such data provide evidence, as we do here, that it may be important to account for prey community composition, as well as for

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inherent preferences, when using selectivity criteria to predict diet of larval yellow perch. Moreover, the importance of community composition to a comparison of larval diet between foraging habitats will only increase as differences in community composition increase, which is more likely with increasing differences in geography and size between systems. Our empirical selectivity model is a strong tool for quantifying these differences so that we can effectively compare different yellow perch populations.

Implications of diet shifts across systems

Different foraging decisions made by larval perch in the model when exposed to nearshore Lake Michigan or Green Bay prey assemblages resulted in large differences in growth and survival. Model results suggest that larval perch in Green Bay grow faster than those in nearshore Lake Michigan at comparable prey densities. The resulting size distribution of survivors indicates that prey density affects how many individuals achieve the maximum observed growth rate, while prey community composition controls the magnitude of the maximum observed growth rate.

The bimodality in the size distributions of larval survivors predicted by the model appears to be the result of an interaction between zooplankton community composition and timing of individual hatch. Larvae that hatched into the model at times when small copepods were abundant selected for copepods at smaller larval sizes than larvae hatched when small copepods were rare relative to other available prey. This diet shift resulted in a higher initial larval growth rate, and this early growth advantage was still detectable in the bimodal size distribution of larvae 30 days after peak hatch. Post et al. (1997) observed a bimodality in the size structure of young perch cohorts in Lake St George, Ontario, in some years but not in others. They attributed this within-cohort size difference to density-dependent competition, but this splitting of a cohort into two size groups is also consistent with an early growth advantage for the part of the cohort that may be related to earlier onset of optimal feeding due to temporal differences in prey community composition.

Our model simulations did not include predation, and the character distributions of survivors would differ if predation mortality had been included. However, the higher predicted growth rate for larvae in Green Bay is also likely to result in lower vulnerability to predation. Based on differences in the size distribution of survivors, larval yellow perch growth rates in Green Bay are predicted to be more variable among individuals, resulting in a higher maximum growth rate among individuals. High growth variability among individuals means that larvae in the upper portion of the growth rate distribution are likely to reach a refuge from size-dependent predation faster; this may increase overall survival (Rice et al. 1993).

Larvae in nearshore Lake Michigan are also predicted to be less responsive to changes in prey abundance than larvae in Green Bay. Starvation rate was over 80% and mean growth rate was less than 0.1 mm·day^{-1} for larvae in both Green Bay and nearshore Lake Michigan at the lowest prey density modeled. Starvation rate decreased and growth rate increased slowly with increasing prey density for nearshore Lake Michigan in the model, and growth rates did not approach growth rates for yellow perch we observed in the field (0.12–0.57 mm·day^{-1}) until prey densities exceeded 150 prey·L^{-1}. In contrast, both growth rate and starvation rate of larvae exposed to a prey assemblage from Green Bay improved more rapidly as prey density increased.

Many of the larvae predicted to starve in our model would likely be eaten before they starved to death in the natural world. The significance of our results is that in years when other forms of mortality such as predation are low in Green Bay, larval survival will likely be high, but variability in these other forms of mortality will have a less consistent effect on larval recruitment in nearshore Lake Michigan. Larval survival in nearshore Lake Michigan is primarily dependent on larvae finding high-density patches of prey to grow. Historical examinations of zooplankton density in Lake Michigan suggest this is less likely now than it was in the late 1980s when yellow perch recruitment was high (Dettmers et al. 2003). A strong initial dependence on foraging success means that in years when larval overlap with optimal prey is low, year-class strength will likely be low, but in years when this overlap is high, year-class strength could be high or low, depending on the importance of other forms of mortality. Consequently, good larval survival and a subsequent strong year class will occur less often in Lake Michigan than in Green Bay, increasing the dependence of longer-term population stability for yellow perch in Lake Michigan on extrinsic factors affecting larval survival.

These conclusions are based on prey community differences at a large scale (i.e., between systems). We did not attempt to take into account small-scale factors such as changes in foraging efficiency due to water clarity or turbulence. Furthermore, because we are comparing the zooplankton assemblages of Green Bay in 1998–1999 to nearshore Lake Michigan 2000–2001, we cannot make predictions about the year class in Green Bay being better than that in Lake Michigan in any particular year. Nonetheless, by studying the effect of community composition across multiple years and a range of zooplankton densities, it is possible to address the larger questions of whether differences in prey composition between systems are important to differences in larval survival and whether a single model of foraging behavior is sufficient to describe larval diet across a range of prey communities. Our model results suggest this is the case.

We did have to make several simplifying assumptions within the IBM framework. Most of these are part of the general IBM framework and have been well addressed previously (Letcher et al. 1996; Fulford 2003). In particular, larval foraging activity was assumed to be evenly spread across the day, and no feeding was assumed to occur at night. These assumptions are reasonable based on observations of yellow perch larval activity in tank systems (R. Fulford, unpublished data). Further, both predator and prey were assumed to be evenly distributed in space, and while this assumption may not always be true in nature, it is a reasonable simplification for comparisons of larval growth across systems.

It is important to have an understanding of how different factors affecting growth and survival of yellow perch populations may differ in importance between systems prior to making comparisons between those systems. Factors found to be important to growth and survival of larval yellow perch in smaller systems include density dependence (Post and McQueen 1988; Sanderson et al. 1999), predation (Campell

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1998; Mayer et al. 2000), interspecific competition (Roseman et al. 1996), and overwinter mortality (Post and Evans 1989). Owing to the size and depth of Lake Michigan, density-dependent effects are going to be ameliorated by larval dispersion, and long-term survey data indicate that year-class strength is highly correlated with juvenile abundance in the fall (Clapp and Makauskas 2002), which suggests that overwinter mortality is not an important factor. The importance of predation and competitive interactions with other species such as alewife remains open. Nevertheless, our results suggest that the interaction of prey community composition in Lake Michigan with larval yellow perch selectivity patterns results in a strong relationship between prey availability and larval survival not observed in smaller systems.

Yellow perch life history seems optimized for smaller, more productive systems where survival during the pelagic phase is more consistent between years. For populations of yellow perch in systems such as Green Bay or Oneida Lake that exhibit higher larval survival (Mayer et al. 2000), population regulation is more dependent on factors regulated by perch density, such as overwinter mortality or predation during the juvenile stage (Mayer et al. 2001). In Lake Michigan, where annual recruitment appears dependent on density-independent factors such as spatial and temporal overlap with prey, recruitment patterns observed in smaller systems would have less value for predicting annual recruitment. In such cases, the individual-based modeling approach is a valuable and flexible tool for a comparative assessment of factors important to larval survival.

For larval yellow perch, the importance of diet choice constrained by limited foraging ability (e.g., first feeding) and limited availability of optimal prey items (e.g., Lake Michigan) can be both strong and important for describing patterns in annual recruitment success. Under these conditions, it is vital to describe changes in larval prey community composition in both time and space in Lake Michigan to better characterize how foraging-mediated recruitment patterns may be important to predicting population recovery.

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Distribution, abundance, and diversity of stream fishes under variable environmental conditions

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Abstract: The effects of stream size and flow regime on spatial and temporal variability of stream fish distribution, abundance, and diversity patterns were investigated. Assemblage variability and species richness were each significantly associated with a complex environmental gradient contrasting smaller, hydrologically variable stream localities with larger localities characterized by more stable flow regimes. Assemblages showing the least variability were the most species-rich and occurred in relatively large, stable environments. Theory suggests that species richness can be an important determinant of assemblage variability. Although this appears to be true in our system, we suggest that spatial and temporal heterogeneity in the environment largely determines both assemblage richness and variability, providing a more parsimonious explanation for the diversity–variability correlation. Changes in species richness of local assemblages across time were coordinated across the landscape, and assemblages formed spatially and temporally nested subset patterns. These results suggest an important link between local community dynamics and community-wide occurrence. At the species level, mean local persistence was significantly associated with regional occurrence. Thus, the more widespread a species was, the greater its local persistence. Our results illustrate how the integrity of local stream fish assemblages is dependent on local environmental conditions, regional patterns of species distribution, and landscape continuity.

Résumé : Nous avons étudié les effets de la taille du cours d'eau et du régime des eaux sur la variabilité spatiale et temporelle de la répartition, de l'abondance et des patrons de diversité des poissons dans ce cours d'eau. La variabilité du peuplement et la richesse en espèces sont toutes deux associées significativement à un gradient complexe du milieu, mais de façon différente dans les sites lotiques plus petits à hydrologie variable et les sites plus grands à régime hydrologique plus stable. Les peuplements qui subissent le moins de variabilité sont ceux qui ont la richesse en espèces la plus importante et qui se retrouvent sur les sites plus étendus et plus stables. La théorie écologique indique que la richesse en espèces peut être un important facteur déterminant de la variabilité des peuplements. Bien que cela semble être le cas dans le système que nous avons étudié, nous croyons que l'hétérogénéité spatiale et temporelle du milieu détermine en grande mesure tant la variabilité que la richesse des peuplements, ce qui explique de façon plus parcimonieuse la corrélation diversité–variabilité. Les changements de richesse en espèces des peuplements locaux au cours du temps sont synchronisés sur tout le paysage et les peuplements forment des patrons de sous-ensembles emboîtés spatialement et temporellement. Nos résultats indiquent un lien important entre la dynamique de la communauté locale et l'occurrence à l'échelle de la communauté. Au niveau spécifique, la persistance locale moyenne est associée significativement à l'occurrence régionale. Ainsi, plus une espèce est largement répartie, plus sa persistance locale est grande. Nos résultats montrent combien l'intégrité des peuplements locaux de poissons dépend des conditions locales de l'environnement, des patrons régionaux de répartition des espèces et de la continuité du paysage.

[Traduit par la Rédaction]

Introduction

Two fundamental attributes of a community are the number of species present and their abundance structure. Both attributes are dynamic, and it is logical to expect a relationship between them (Tokeshi and Schmid 2002). Indeed, one of the most hallowed tenets in ecology and conservation biology is the idea that diversity promotes the stability of

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communities and ecosystem processes. This idea can be traced to Elton (1958), who was concerned with the ecological impact of exotic animals and plants on native flora and fauna. It remains equivocal which aspect of diversity (number of species, functional groups, trophic groups, etc.) is the important causal factor, or whether the environment drives patterns of diversity and stability (Sankaran and McNaughton 1999). The stability–diversity question is obfuscated further by much disagreement over the meaning of the term "stability". Grimm and Wissell (1997) identified 163 definitions and 70 different stability concepts.

In spite of these difficulties, the theoretical underpinnings of the stability–diversity hypothesis, as well as the attendant criticism and debate, allow tangible predictions to be made about the structure and function of ecological systems. We know that communities are affected by extrinsic factors (Brown and Lomolino 1998) ranging from historical processes (Cornell and Lawton 1992; Gorman 1992; Williams et al. 2003) to landscape- or regional-level processes (Turner 1989; Schlosser 1991; Pickett and Cadenasso 1995). Recent metapopulation- and macroecology-based studies have focused on identifying landscape-level processes and species-specific life history and ecological traits that may be important in determining various community properties. For example, regional processes, such as immigration and extinction dynamics, can have important effects on local community structure (Taylor and Warren 2001; Cottenie et al. 2003; Warren et al. 2003), and these dynamics may be associated with species-specific traits such as body size, mean local abundance, species–environment relationships, and regional occurrence (Gotelli and Taylor 1999).

In streams (and other ecosystems), interaction between the environment and population processes affects the distribution and abundance patterns of species and, thus, community structure (Brown 1984). Such interactions have been the focus of much research, including studies on species-specific habitat selection, intracommunity interactions, habitat size and complexity, isolation and fragmentation, and immigration and extinction dynamics. However, determining environmental influences on spatial and temporal assemblage patterns is difficult because different spatial and temporal scales yield different types of information (Wiens et al. 1986). Two complex environmental gradients appear to be very important in influencing stream fish assemblages and habitat structure: stream size and the flow regime (Gorman and Karr 1978; Horwitz 1978; Schlosser 1987). Longitudinal zonation or succession of fish assemblages is a well-known phenomenon (see Matthews 1998). A specific pattern embedded in this concept is the increase in the number of fish species from headwaters to higher-order streams (Sheldon 1968; Schlosser 1987; Rahel and Hubert 1991). This pattern often is attributed to a general increase in habitat size and heterogeneity, coupled with reduced variability in flow regime that occurs from upstream to downstream. These patterns are altered by habitat fragmentation at different scales. Locally, low flows may promote isolation of habitats that are connected during periods of ambient or high flows. At larger spatial scales, dams and channelization alter stream habitat and flow regime and reduce or curtail routes of dispersal. Thus, stream size and flow regime, as well as the disruption of these factors by fragmentation at multiple scales, may be the most important drivers of observed patterns of assemblage stability and diversity of fishes in stream systems.

Taylor and Warren (2001) found that occupancy of local sites across time formed significant nested subset patterns at nine of the 12 localities from our study system. A nested subset pattern occurs when species-poor samples form subsets of species-rich samples, such that rare species (low incidence) occur only in the richest samples and common species (high incidence) occur in samples with a wide range of richness values. This highly structured temporal pattern indicated a gradient regarding local persistence of species. The strength of the nested pattern was strongly associated with local extinction rate, indicating a deterministic nature to the local extinction process. Additionally, there was spatial structure to immigration and extinction processes. Immigration rates were highest at large stream localities, and extinction rates were highest where variability in the flow regime was high (headwater localities).

Based on the development of these concepts and the theory behind them, we had two major objectives in this study. For the first objective, we used an assemblage-based approach designed to identify important spatial and temporal trends in assemblage properties (structure, species richness, variability) and relate these to the underlying environmental template. To meet this objective, we examined relationships among assemblage structure, assemblage variability, species richness, and the spatial and temporal variability of the environment in our system. We predicted that assemblage properties would each show strong responses to gradients of stream size and flow variability and that environmental influence would render trivial any relationship that may occur between species richness and assemblage variability. Furthermore, given the temporally nested patterns of local persistence that Taylor and Warren (2001) found, we predicted that fluctuations in local species richness would be correlated across the landscape, suggesting a common response by assemblages to changing environmental conditions. Likewise, we also predicted that species-richness patterns across the landscape would form nested subset patterns and be strongly correlated through time. Such nonrandom, coordinated patterns in space and time would suggest an important link between local community assembly and community-wide occurrence patterns.

For our second objective, we used a species-based, macroecological approach to examine the relationships among species-specific properties, including regional occurrence, mean local abundance, and mean local persistence. Species vary with regard to their life history and ecological traits (Gotelli and Taylor 1999), and the structure of assemblages within a region is, in part, because of this inherent species-specific variation. If assemblages exhibit coordinated patterns in space and time, it is reasonable to presume a relationship between locally and regionally expressed attributes of species. For example, the positive association between regional occurrence and mean local abundance is a well-documented pattern for a wide variety of systems (Hanski et al. 1993; Gaston et al. 1997; Hughes 2000), and we predicted the same from our system. Further, if assemblages exhibit nested occurrence patterns in space (regional scale) as they have been shown to do in time (local scale), we hypothesize that species will show a positive association between

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regional occurrence and local persistence. Delcourt et al. (1983), Wiens (1989), and Holling (1992) have all suggested that there is congruence between spatial and temporal scales in ecological processes. Such a pattern would have obvious and important conservation and management implications (Bissonette and Storch 2002), especially in highly fragmented systems where dispersal corridors are upset.

Materials and methods

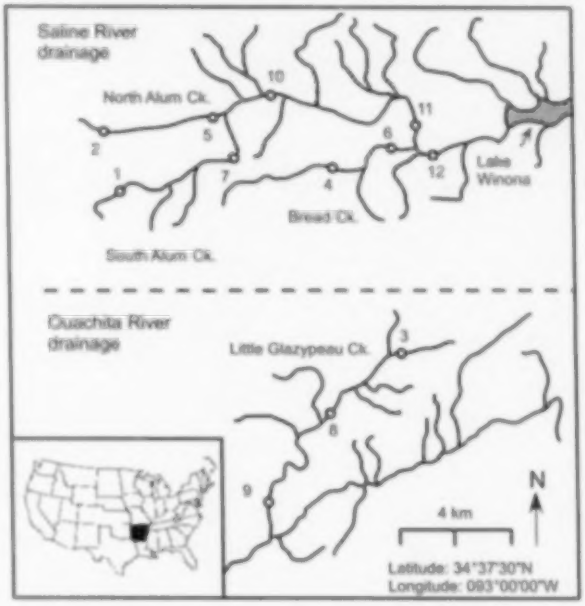
Study area

The Ouachita Mountains of Arkansas and Oklahoma are characterized by strongly folded, uplifted, sedimentary rock and pine–oak upland forest (Robison 1986). Our sample sites were located in two river systems within the Red River drainage on the eastern side of the uplift. Nine sites were located in the Alum Fork of the Saline River (hereafter Alum Fork) and three sites were in Little Glazypeau Creek of the Ouachita River system (Fig. 1). Both systems are high gradient with strong riffle–pool development. The water is generally clear except after extensive precipitation events (terrestrial runoff) and during drought (increased primary productivity in isolated pools). Pools ranged from a few metres to ≥50 m in length and, under ambient conditions, are separated by swift riffle habitats consisting of coarse substrate materials. These streams are characterized by high variability in the flow regime. Water levels can rise and fall rapidly with heavy precipitation events, and headwater reaches are intermittent, frequently drying to isolated pools during summer and autumn months. Thus, habitats and their corridors can grow, shrink, and change configuration rapidly (Taylor 1997; Taylor and Warren 2001; Williams et al. 2003). These small, hydrologically dynamic streams provide an ideal system to address questions concerning the effects of environmental variability on distribution and abundance patterns of fishes.

Data collection

From November 1995 through August 1998, we sampled fishes and measured environmental variables at 12 sites (144 total samples; Fig. 1). We sampled in November, February, May, and August in each year and always completed sampling within 3–4 days. At each site, we electrofished all habitat types within a 100 to 200 m stream reach (depending on stream size) that spanned at least two pool–riffle sequences. For stream fishes, the stream reach is a logical sample unit in a river system (Frissell et al. 1986), and the effects of disturbance on assemblage-level properties are measured most commonly at this scale (see Matthews 1998). The same individual (CMT) always operated the backpack electroshocker (model 12-A; Smith-Root Inc., Vancouver, Washington), and there were always two to three netters present to capture stunned fishes. Riffles were sampled from bottom to head, and runs and pools were sampled in a downstream direction. Because of the small size and clear water, we were able to sample stream reaches and all habitats therein efficiently. We opted for a representative reach approach (Frissell et al. 1986; Williams et al. 2004) and the increased spatial coverage rather than using intensive multipass procedures that would have required greater effort per habitat and a reduced reach length (see Taylor and Warren 2001). After sampling a site, we identified and counted all fishes and returned them to the stream alive.

Fig. 1. Map showing the 12 study sites in south-central Arkansas, USA. Numbers represent rank in catchment area. The broken line indicates that geographic proximity of the two drainages is not as shown. Both drainages occur in the Red River system.



After fish sampling and processing, we measured habitat variables along transects (perpendicular to stream flow) spaced at 10 to 15 m intervals along the sampled stream reach. The number of transects varied (eight to 12) depending on the length of the sampled stream reach. We permanently marked transects and resurveyed them during each visit. At every other metre along transects, we measured current velocity, depth, and dominant substrate type. We categorized substrate following Taylor and Lienesch (1996*a*, 1996*b*) as bedrock, large boulder (>300 mm), small boulder (150–300 mm), cobble (50–149 mm), gravel (3–49 mm), or sand (<3 mm). We measured stream width at each transect and noted the presence or absence of aquatic macrophytes, algae, undercuts, and woody debris.

Data treatment and analyses

Stream size is a complex variable and many features of the environment often are used as its surrogate. For each site, we measured upstream catchment area, and for each sample (site–date), we determined means and maxima for stream width, stream depth, and current velocity. We then averaged these values to get site-specific measures of width, depth, and current speed across the three years. We log-transformed these environmental variables before analyses to improve normality and linearity. Because we also were interested in the temporal variation displayed by our measured environmental variables, we calculated coefficients of variation (CVs) for each site across sample dates for all width, depth, and current velocity variables.

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To quantify spatial heterogeneity in our measured variables at each site, we chose one sample period in the spring (May 1997) and used the point substrate, depth, and current speed measurements to estimate variation within each site. For substrates, we used the Shannon–Weiner diversity index to calculate a measure of substrate heterogeneity for each site. For current speed and depth, we calculated CVs based on all point estimates.

Unless otherwise noted, we calculated local species richness as the total number of species collected across the entire study period at a site. This cumulative measure of species richness estimates the "realized species pool" for individual sites (Taylor and Warren 2001). For the macroecological analyses of species-specific traits, we limited our data to the nine sites in the Alum Fork drainage. We determined the regional occurrence of each species by totaling the number of occupied sites in the study area, regardless of the number of occupied samples at a site. For each species, we also counted the number of occupied samples for each site and averaged these numbers to obtain a mean local persistence. To calculate mean local abundance, we summed abundances across samples for each species and averaged these across all occupied sites.

To summarize the fish assemblage data and quantify the effects of stream size and habitat variability on fish assemblages, we used univariate and multivariate statistical methods. We conducted ordinations with PC-ORD software (B. McCune and M.J. Mefford 1995). We performed all other data analyses with SYSTAT (SPSS Inc. 2000), EcoSim (Gotelli and Entsminger 2001), and the Nestedness Temperature Calculator (Atmar and Patterson 1995).

We used nonmetric multidimensional scaling (NMS) to provide a convenient and interpretable picture of fish assemblage change across spatial and temporal gradients. NMS is an indirect ordination technique designed to summarize complex community data (Gauch 1982). Because it is not based on any distributional assumptions (McCune and Grace 2002), NMS is well suited for use with ecological data and is not plagued with problems of other ordination methods such as correspondence analysis and detrended correspondence analysis (Wartenburg et al. 1987; Jackson and Somers 1991; Legendre and Legendre 1998). The technique is based on an iterative search algorithm that minimizes departure from monotonicity in the relationship between dissimilarity in the original data matrix and distances in the reduced ordination space (McCune and Grace 2002).

We used NMS on two data sets: in the first, we ordinated all samples to assess temporal variation in assemblages at each site, and in the second, we summed abundances at each site to examine among-site differences in overall assemblage structure. Before running the NMS procedure, we square-root-transformed fish abundance data and computed Bray–Curtis distances among all sample units. We followed the general NMS procedure outlined by McCune and Grace (2002, pp. 135–136).

To quantify assemblage variability at sites, we calculated all pairwise Bray–Curtis distances across all samples for each site and then used the average distance as an overall site-specific measure of variability. The Bray–Curtis distance is sensitive to changes in species abundance (Wolda 1981), a desirable trait for our purposes. Absolute and relative changes in abundance are both sources of assemblage variability that we wanted to quantify among samples for a given site. Beals (1984) highly recommended the Bray–Curtis distance based on its success over a wide range of ecological systems (Ludwig and Reynolds 1988). We then used linear regression to assess the relationship between assemblage variability and species richness.

Principal components analysis (PCA) was used on all stream size variables and associated CVs to identify the primary environmental gradients in the system. These gradients were then used in regression analyses to test our hypothesis that assemblage structure, diversity, and variability patterns would be strongly associated with local environmental conditions.

Because our regression analyses assume independence of data points (sites), we first examined our variables for spatial patterning using the Mantel test. First, pairwise stream distances (km) were measured among sites (Alum Fork drainage). Difference matrices were then constructed for all variables and matrix correlations were computed with the geographic matrix. Significance was assessed with a Monte Carlo procedure (Fortin and Gurevitch 1993) based on 5000 permutations.

We used Atmar and Patterson's (1993) T (temperature) to assess the degree of nestedness across the landscape for each sampling period in the Alum Fork system. Their T is well correlated with other measures of nestedness that have been proposed in recent years (see review by Wright et al. 1998). The T is derived from entropy and information theory and describes the unexpected presences and absences of species in a matrix that has been packed into a state of maximum nestedness. A T of 0° defines complete order and perfect nestedness, whereas a T of 100° would result from a completely random matrix. We used a Monte Carlo procedure (5000 randomizations) to assess the probability that such a distribution pattern could occur by chance. Fischer and Lindenmayer (2002) found that T was prone to Type I errors but cautioned that other methods may be prone to Type II errors. Thus, we conservatively set α at 0.01 for our nestedness analyses. In a review of null models, Gotelli (2000) discussed different types of errors that may affect the significance of various null models.

Finally, we assessed site-specific change in the species richness of samples in the Alum Fork system (nine sites) across all time periods and compared these patterns across the landscape with Kendall's coefficient of correlation. Likewise, we use the coefficient to assess changes in landscape patterns of species richness across time.

Results

We collected a total of 30 fish species (and numerous individuals of a hybrid sunfish, *Lepomis megalotis* × *cyanellus*) from the 12 sites. Species varied greatly in their overall relative abundances and distribution across sites (Table 1). At the coarsest level, five species were collected only from the Little Glazypeau system, and six species were collected only in the Alum Fork system. Large-scale historic differences in geomorphology, speciation, extinction, and dispersal account for the nonshared components between the regional assemblages (Cross et al. 1986). The two systems

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Table 1. Species, occurrences in the two drainage systems, relative abundances, and Pearson correlations of species with the first two axes from a nonmetric multidimensional scaling (NMS) analysis on the species-by-site summed abundance matrix.

Species	Alum Fork	Little Glazypeau	Percent abundance	NMS 1 (0.50)	NMS 2 (0.47)
Ameiurus natalis	5	2	<0.01	–0.73	0.60
Aphredoderus sayanus	8	1	0.01	–0.39	–0.57
Campostoma anomalum	8	3	0.18	–0.86	0.61
Chaenobryttus gulosus	1	0	<0.01	–0.33	0.03
Erimyzon oblongus	9	3	0.04	.01	–0.75
Esox americanus	8	2	0.01	–0.16	–0.68
Etheostoma blennioides	2	1	<0.01	–0.57	0.31
Etheostoma collettei	6	0	0.07	–0.68	–0.14
Etheostoma radiosum	0	3	0.05	–0.04	0.81
Etheostoma whipplei	9	0	0.09	0.21	–0.86
Fundulus catenatus	0	2	0.01	–0.24	0.73
Fundulus olivaceous	7	3	0.05	–0.89	0.18
Hypentelium nigricans	0	2	<0.01	–0.25	0.73
Ichthyomyzon gagei	3	0	<0.01	–0.56	–0.02
Labidesthes sicculus	6	0	0.01	–0.67	–0.08
Lepomis cyanellus	9	3	0.07	0.29	0.35
Lepomis hybrid	5	0	<0.01	–0.06	–0.57
Leopmis macrochirus	5	3	0.01	–0.43	0.47
Lepomis megalotis	8	3	0.19	–0.93	0.34
Lythrurus umbratilis	7	3	0.07	–0.55	–0.01
Luxilus chrysocephalus	0	3	0.01	–0.15	0.81
Micropterus dolomieu	0	1	<0.01	–0.25	0.49
Micropterus punctulatus	4	2	<0.01	–0.72	0.43
Micropterus salmoides	3	2	<0.01	–0.35	0.24
Notropis boops	6	1	0.02	–0.51	–0.01
Notropis ortenburgeri	3	0	0.01	–0.23	–0.33
Noturus nocturnus	0	1	<0.01	–0.25	0.49
Noturus lachneri	7	0	0.05	–0.66	–0.29
Percina caprodes	4	1	0.01	–0.64	0.41
Pimephales notatus	4	1	0.02	–0.60	0.19
Semotilus atromaculatus	7	2	0.04	0.72	–0.10

Note: Parentheses indicate coefficient of determination for the correlations between ordination distances and dissimilarity in the original distance matrix.

are adjacent, separated by an east–west trending ridge, and both drain into the Red River but are isolated by long distances of lowland, big-river habitat. The effectiveness of this isolation is demonstrated by the evolution of one endemic species (*Noturus lachneri*, Alum Fork system). Within both drainages, abundances and occurrences were highly variable across space and time, reflecting the different ecological conditions along the stream continuum (Table 2).

Two gradients of stream size and flow variables accounted for 50% (PC1) and 20% (PC2) of the variation in the PCA of the environmental variable-by-site data matrix. The first gradient (PC1) contrasted small, intermittent, headwater streams with larger, more heterogeneous, and less hydrologically variable streams (Table 3). The second gradient (PC2) was associated primarily with temporal variability in stream width and depth.

The structure of site-specific assemblages across time showed considerable variability (Fig. 2), but between basin assemblages were distinctive (Fig. 3). The overall large spread of points in the two-dimensional NMS space was indicative of high variability among the sites (Gauch 1982). This was especially evident when comparing sites from the Little Glazypeau system (sites 3, 8, and 9) with sites from the Alum Fork system. By summing abundance for each site, thus collapsing the variation across time, the two drainage basins were clearly separated (Fig. 3). For a given locality, the variability (represented by the spread of sample points in the two dimensional space) was considerably less across time at larger, downstream sites compared with smaller, upstream sites (Figs. 1 and 2). Despite variability in assemblage structure for each site across time, each locality was confined to a relatively small proportion of the overall two-dimensional ordination plot (Fig. 2).

Species correlations with both NMS axes indicate their relative importance across the 12 localities (Table 1). For example, *Campostoma anomalum*, *Fundulus olivaceus*, and *Lepomis megalotis* were all relatively common species that had strong negative correlations with the first axis, thus indicating their importance at sites on the left side of the ordination plot in Fig. 3. *Etheostoma radiosum* and *Luxilus*

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Table 2. Substrate characteristics (percent composition of point estimates), mean stream width, mean stream depth, and mean stream current speed for the 12 sampled localities.

	Substrate								
Sites	Sand	Gravel	Cobble	Small boulder	Large boulder	Bedrock	Mean width (m)	Mean depth (cm)	Mean velocity ($m \cdot s^{-1}$)
1	0	10	23	45	23	0	3.7	30.0	0.02
2	0	30	25	15	10	20	2.6	16.7	0.07
3	0	62	31	4	0	4	2.8	22.1	0.05
4	0	3	53	29	15	0	4.0	29.1	0.13
5	0	0	43	36	14	7	3.7	21.9	0.15
6	0	3	21	21	9	47	6.0	30.0	0.07
7	0	16	16	42	26	0	6.7	40.0	0.09
8	3	26	43	23	3	0	4.9	28.6	0.13
9	0	34	6	23	37	0	11.3	34.7	0.13
10	8	11	70	11	0	0	4.9	34.0	0.14
11	0	0	21	38	41	0	7.9	36.1	0.19
12	0	18	33	24	6	18	10.8	39.4	0.15

Note: Substrate composition is reported for November 1996 samples under ambient flow conditions. Means for other variables are calculated across the entire study period. Stream locality numbers correspond to rank in upstream catchment area and Fig. 1.

Table 3. Loadings for first two principal components.

	Component loadings	
Variables	PC1 (49.7)[a]	PC2 (19.6)[a]
Upstream watershed area	0.93	–0.5
Maximum depth	0.90	0.28
Maximum current speed variability[b]	–0.90	–0.01
Width	0.88	0.30
Maximum current speed	0.86	–0.12
Maximum width	0.83	0.49
Depth	0.80	0.46
Permanence	–0.77	0.17
Current speed	0.75	–0.53
Current speed heterogeneity	0.75	–0.37
Depth heterogeneity	0.64	0.62
Maximum depth variability	–0.36	0.75
Depth variability	–0.40	0.72
Maximum width variability	–0.47	0.61
Current speed variability	–0.49	–0.12
Width variability	–0.21	0.35
Substrate heterogeneity	0.45	0.28

[a]Percent variance accounted for is given in parentheses.
[b]Variability expressed as the coefficient of variation.

chrysocephalus had strong positive correlations with the second axis and occurred only at Little Glazypeau sites (top of the ordination plot), but *E. whipplei* was correlated negatively with this axis and only occurred at Alum Fork sites.

Results from the Mantel tests to evaluate spatial structure were all insignificant. The strongest relationship occurred for assemblage variability (matrix $r = 0.28$, $P = 0.07$). Thus, we assumed independence of sampling localities for regression and correlation analyses.

As predicted by the stability–diversity hypothesis, assemblage variability and species richness were associated significantly with each other ($r = -0.76$, $P = 0.006$; Fig. 4), but only after removal of an outlier site. This site was the smallest and most variable with respect to flow, but it had a permanent refuge pool that held water throughout the study period. The refuge moderated the local extinction process (Taylor and Warren 2001) and provided a relatively high level of assemblage stability, even under conditions of high environmental variability.

However, as we predicted, the primary environmental gradient (PC1) significantly explained species richness ($r = 0.86$, $P < 0.001$; Fig. 5*a*) and assemblage variability ($r = -0.54$, $P = 0.07$; Fig. 5*b*). Removal of the same outlier site improved the relationship between the environmental gradient and the assemblage variability ($r = -0.72$, $P = 0.012$). Thus, larger, less variable (e.g., flow regime) stream localities had greater species richness and generally exhibited less assemblage variability through time. Assemblages were structured strongly along this environmental gradient as well. The first PC was associated strongly with the first NMS axis ($r = -0.92$, $P < 0.0001$; Fig. 5*c*). The second PC was not associated significantly with species richness, assemblage variability, or assemblage structure. With all assemblage properties responding strongly to the environmental gradient, it was not surprising that temporal (mean Bray–Curtis distances) and spatial (NMS axis 1) assemblage properties were strongly associated ($r = 0.74$, $P = 0.010$).

Sites in the Alum Fork watershed showed strong and significant ($P < 0.01$) nested subset patterns for 11 of the 12 sample periods (mean $T = 21.3°$, range = 14.5°–29.0°). Only the summer 1998 samples produced a relatively weak pattern of nestedness ($T = 30.8°$, $P = 0.015$). When all samples at a site were summed to include the realized species pool, the T value remained low and highly significant ($T = 22.04°$, $P < 0.0001$), with sites furthest downstream containing the rarest species. There was no significant difference among seasons for T values or standard deviation units (δ) of observed T values from the mean of the randomized values (T, $F = 0.479$, $P = 0.706$; & $F = 0.615$, $P = 0.624$). Local species richness values across the landscape were correlated through time (Kendall Coefficient of Concordance = 0.34, $P = 0.0004$), and fluctuations in local species richness were correlated across the landscape (Kendall Coefficient of Concordance = 0.80, $P < 0.00001$).

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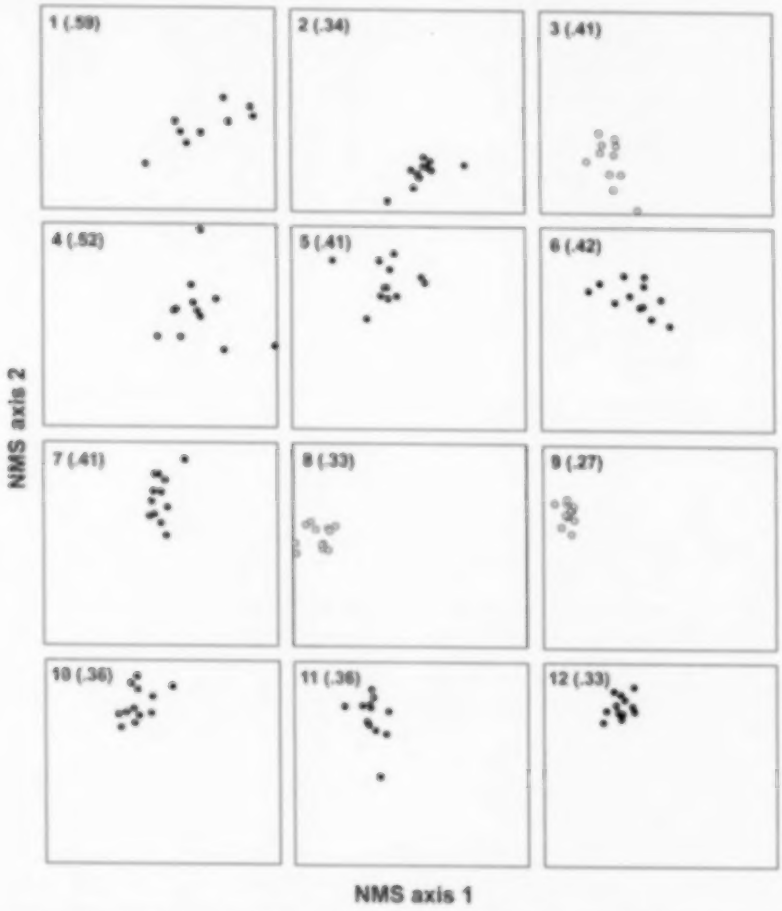
Fig. 2. Nonmetric multidimensional scaling (NMS) ordination of all sites and samples across the 3-year period. Sample scores are plotted in multivariate space defined by NMS axes 1 and 2. Numbers correspond to Fig. 1 and represent rank in catchment area and average Bray–Curtis distance among all samples at a site (parentheses). ●, Alum Fork sites; ○, Little Glaypeau sites. Scaling is equivalent among plots.



Mean local abundance across species was associated positively with regional occurrence ($r = 0.535$, $P = 0.006$), and the observed shape of the points was triangular with a significant boundary (observed points within space = 22, mean of 5000 simulated runs = 19.65, variance of simulated points = 1.22, $P = 0.037$; Fig. 6). Mean local abundance also was associated strongly with mean local persistence rates ($r = 0.80$, $P < 0.0001$) such that the more locally abundant a species was, the greater its chance of persisting at localities (Fig. 7). Finally, regional occurrence was associated positively with mean local persistence ($r = 0.67$, $P = 0.0003$), and this relationship was retained after factoring out the influence of local abundance on local persistence (partial $r = 0.47$, $P = 0.020$; Fig. 8).

Discussion

Assemblage structure, variability, and diversity

Ecological communities are assembled and maintained by a variety of factors and processes, including historical contingency, spatial and temporal aspects of the environment, and species interactions (Pianka 1994). For many systems, complex habitats generally support more species than homogeneous habitats. Increased habitat heterogeneity provides a greater variety of resources for species, possibly reducing competition through resource partitioning (Schoener 1988). For stream fishes in headwater streams, habitat heterogeneity is associated positively with species diversity, and both factors tend to increase along the downstream gradient (Sheldon 1968; Gorman and Karr 1978; Schlosser 1987). In our system, three groups of variables showed significant changes from upstream to downstream. Habitat size and heterogeneity were associated positively with the upstream to downstream gradient, but flow variability decreased at downstream localities. Assemblages were strongly structured along this gradient and were more species-rich and less variable in relatively stable, heterogeneous, downstream habitats.

Ecologists have developed a large body of theory to understand and explain patterns of community organization and gradients in species diversity. Levins (1968) and MacArthur (1972) formulated a model based on the concept that

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Fig. 3. Nonmetric multidimensional scaling (NMS) ordination of all sites. Abundance data are summed across samples for each site. Sample scores are plotted in multivariate space defined by NMS axes 1 and 2. Labels corresponds to Fig. 1. ●, Alum Fork sites; ○, Little Glaypeau sites. The broken line indicates separation of the two drainages along NMS axis 2.

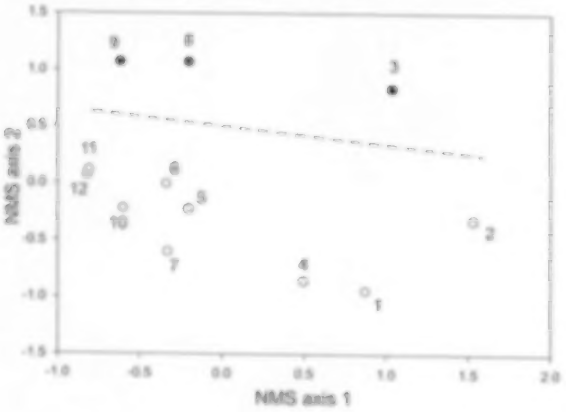
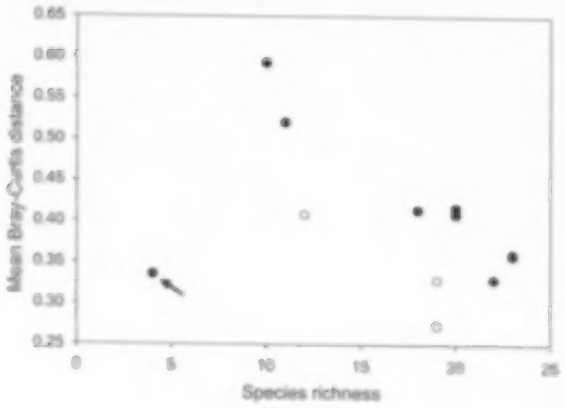


Fig. 4. Relationship between assemblage variability (Bray–Curtis distance) and species richness. ○, sites from the Little Glazypeau system; ●, sites from the Alum Fork system. The arrow indicates an outlier locality (site 2).



persistence in a community is tied to resource specialization and environmental stability (Leigh 1990). Generally, a benign environment should promote specialization and increased "species packing" (after MacArthur 1972) and should support more stable assemblage dynamics. This suggests a positive relationship between environmental stability and species diversity and predicts that more stable environments support more species-rich assemblages. The model of MacArthur and Levins has been highly criticized (Leigh 1990), in large part because of its foundation in competition theory and the assumption that communities exist in a competitive equilibrium. Further, measuring or even defining ecological specialization is very difficult. These criticisms, along with observations that disturbance can reduce or maintain diversity, depending upon its frequency or intensity (Connell 1978), diminished interest in competition as an organizing force in communities (Leigh 1990).

Huston (1979) developed a nonequilibrium hypothesis to explain community diversity that incorporates two important and interacting gradients: disturbance and competitive ability. His model predicts diversity to be highest where competitive displacement and disturbance frequency or intensity are low. The model provides a basis for understanding how disturbance allows coexistence of species but was criticized for not addressing traits or features of species that allow for coexistence (Leigh 1990).

Though conceptually straightforward, competitive ability and ecological specialization are operationally difficult. How does one quantify these concepts? If we assume that habitat heterogeneity (a measurable concept) reduces competitive displacement and promotes ecological specialization, both of the above models become more tractable. Another difficulty pertains to the time scale on which competition and environmental variability may interact to cause divergence and specialization. The theoretical basis of the Levins and MacArthur model assumes an evolutionary time frame, but plasticity in resource use and (or) species-specific traits in response to disturbance or biotic interactions is well known (Werner and Hall 1976; Komer 1997; Werner and Peacor 2003), making the theory applicable at ecological time scales. Mechanisms involving resource specialization were not investigated in this study, but there is support for the idea that resource specialization may increase along the downstream gradient. Taylor (2000) found that riffle and pool assemblages diverged in structure along the stream gradient in several Ouachita Mountain streams. Larger stream localities had more distinct riffle and pool assemblages, whereas in smaller, headwater streams, riffle and pool assemblages converged in structure and riffle habitats were ephemeral.

Nested assemblages, regional occurrence, local abundance, and persistence

The primary gradient in community structure (NMS axis 1) within the Alum Fork watershed was strongly associated with species richness ($r = 0.97$), and assemblages across the watershed were strongly nested, such that the rarest species occurred at the largest, downstream-most sites. These combined results provide strong evidence for a nested community structure, notwithstanding the potential limitations of the various measures of nestedness (Leibold and Mikkelson 2002).

Rare has two meanings in the context of this study: one is based on regional occurrence and the other is based on local abundance. Species can have low or high local abundances if widely distributed, though species rare in occurrence tended to have low local abundances. For example, *Ameiurus natalis* and *Aphredoderus sayanus* were found at most sites but accounted for very little of the total catch with average local abundances of 3 and 9.5, respectively. However, *Lepomis megalotis*, also very widespread, accounted for about 20% of the total catch and had an average local abundance of 133.5. This distribution and abundance pattern produced a triangular dispersion of species in a bivariate plot of regional occurrence as a function of mean local abundance. A positive association between occurrence and abundance is well documented from a number of different systems (Hanski et al.

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Fig. 5. Relationship between the environmental gradient (PC1) and three assemblage properties: (*a*) species richness, (*b*) assemblage variability (Bray–Curtis distance), and (*c*) assemblage structure (NMS axis 1). ○, sites from the Little Glazypeau system; ●, sites from the Alum Fork system.

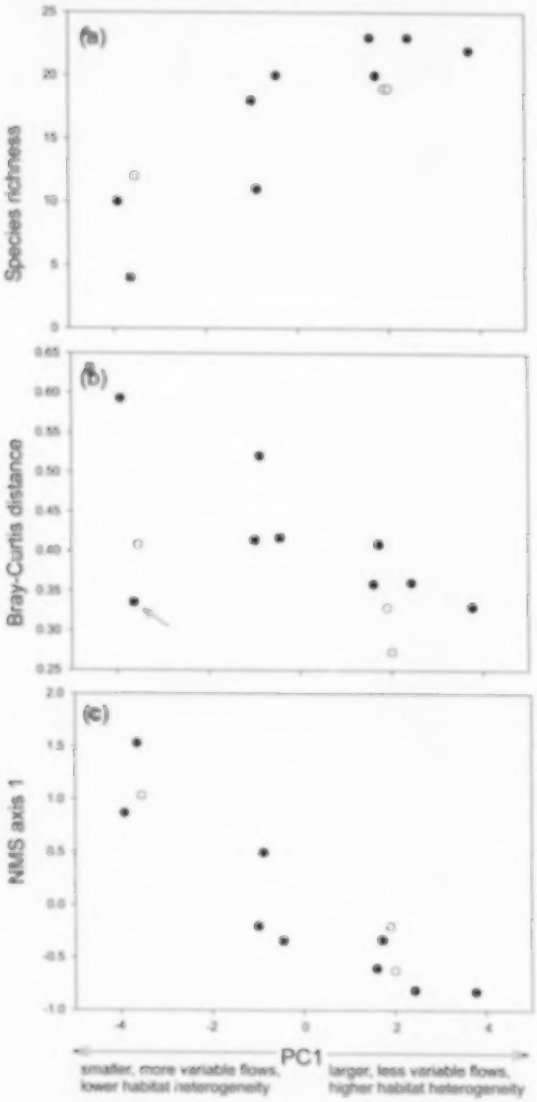


Fig. 6. Relationship between mean local abundance and regional occurrence for all species in the Alum Fork system (nine sites). The broken line indicates a boundary set by the limits of the data (min *x*, min *y*), (max *x*, max *y*).

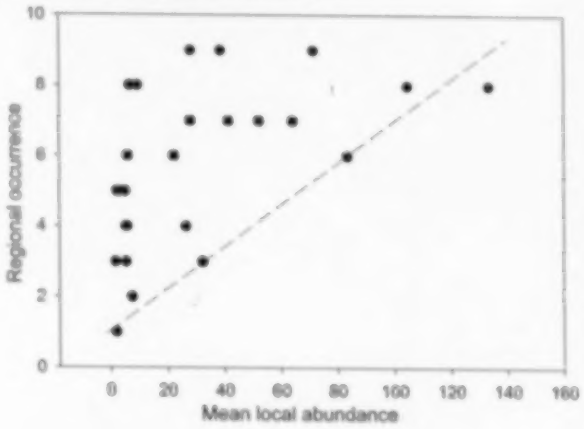
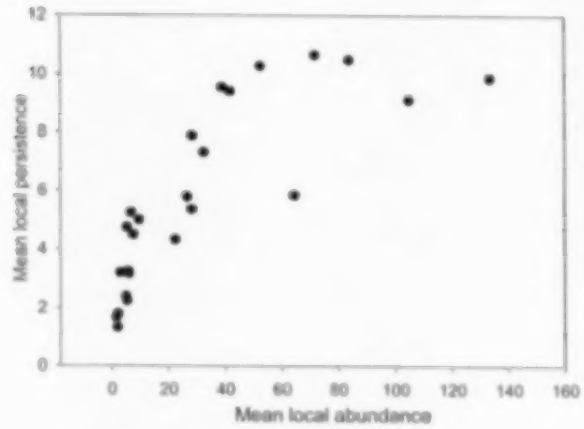


Fig. 7. Relationship between mean local persistence and mean local abundance for all species in the Alum Fork system (nine sites).



1993; Gaston et al. 1997; Hughes 2000), and at least eight hypotheses have been put forth to explain this relationship (Gotelli and Taylor 1999). Recently, it has been shown how this pattern can result from the density and spatial distribution of species that are structured as metapopulations (He et al. 2002). The triangular dispersion we show with our data is novel and indicates that with thorough and repeated sampling, widespread and rare species are eventually sampled and fill out the upper left corner of the bivariate space. Notably, the dispersion pattern implies that unmeasured variables are constraining widespread but locally rare species from approaching the boundary. Given our data, we are unable to identify the nature of these species-specific constraints but suggest they may be related to habitat limitation, biotic interactions, or both.

Taylor and Warren (2001) showed that local abundance was associated strongly with immigration and extinction rates in this system. Thus, we correctly anticipated a strong positive relationship between mean abundance and mean persistence rates, such that species with high local abundances tended be the most persistent at localities. Local persistence of species manifested as a temporally nested subset pattern at seven of nine sites in the Alum Fork system (Taylor and Warren 2001). The strength of the nested pattern was associated positively with local extinction rates, which were determined by stream size and flow variability. In this study, we also show the converse pattern: significant nested subsets occurred across space for each sample date and for summed

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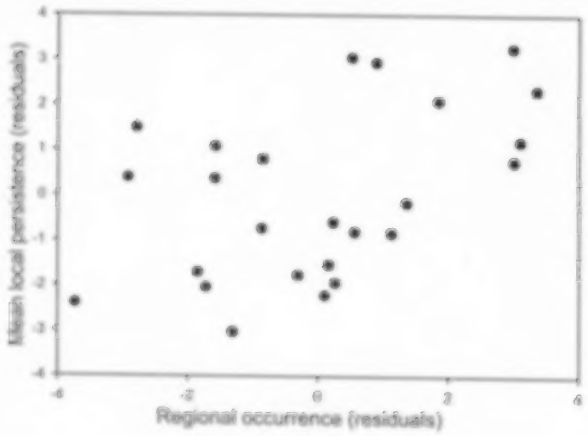
Fig. 8. Relationship between mean local persistence and regional occurrence for all species in the Alum Fork system (nine sites) after statistically removing the effects of mean abundance from both variables.



samples at each site. Furthermore, all quantified community properties were associated strongly with the stream size and flow variability gradient.

We find it intriguing that nested subset patterns in this system occur across space at the landscape scale (this study) and through time at the local scale (Taylor and Warren 2001) and that both were strongly associated with the environmental template. Further, loss and gain of species at the local scale occurred similarly across the landscape, presumably in response to large-scale seasonal changes in the hydrologic cycle. This consistency in pattern for both space and time scales suggests an important link between local community assembly and community-wide spatial structure. Such a relationship would imply that patterns of occurrence across space and time are fundamentally related to each other. Indeed there was a strong positive relationship such that species with a high frequency of occurrence across the landscape also tended to have high average rates of local persistence. Because mean local abundance accounted for about 64% of the variability in mean local persistence and also was correlated strongly with occurrence, it is possible that the relationship between local persistence and regional occurrence was spurious. However, the relationship remained significant after statistically accounting for the effect of abundance on persistence. These results are consistent with theoretical models implicating the importance of interaction between space and time scales in determining the evolution of dispersal rates in fragmented habitats (Paradis 1998) and with empirical studies that attempt to explain local diversity based on regional processes (Kiflawi et al. 2003).

In conclusion, hydrologic variability and habitat heterogeneity were structured spatially in these low-order Ouachita Mountain stream systems such that smaller headwater stream localities were more variable with respect to flow than larger, more heterogeneous downstream localities. We suggest that this complex environmental gradient is the primary determinant of assemblage diversity and variability in our system. We do not imply that species diversity has no impact on assemblage stability in our system but reiterate the importance of explicitly defining what kind of "stability" is in question. A major goal for ecologists is to identify repeated and general patterns in nature (MacArthur 1972), which is difficult to do if researchers are not on the same page. Future studies examining variability in stream assemblage properties should focus on how these properties change along stream size, hydrologic, and habitat diversity gradients according to various theoretical frameworks. We suggest that revisiting the original ideas put forth by Levins and MacArthur might prove useful, especially in conjunction with Huston's nonequilibrium disturbance-based model. This would involve scrutinizing the biological processes and mechanisms of resource specialization that operate and vary across the environmental template.

In addition, our results suggest that community-wide occurrence may interact with patterns of local persistence for fish species in this fragmented stream system. This spatiotemporal coupling has strong implications for the conservation and management of fragmented river systems. Dams in river and stream systems disconnect entire catchments or watersheds from the remainder of the system. Such isolation from downstream populations may cause the system to eventually "relax" to a lesser regional diversity. Anthropogenic disturbances such as poor watershed management practices (Ross et al. 2001) and natural disturbances such as drought can render entire stream reaches uninhabitable for a given species. Hydrological connectivity controls the transfer of materials and products of ecological processes (Jenkins and Boulton 2003), and rare and (or) sensitive species are at risk to such disturbances. Without opportunity of rescue (Brown and Kodric-Brown 1977) from the contiguous stream landscape, they are possibly doomed to regional extinction. Thus, we emphasize the importance of maintaining landscape linkages at multiple spatial scales. The highly variable flow regime in our system causes seasonal fragmentation within the catchment and impacts immigration and extinction dynamics, whereas a dam on the mainstem represents fragmentation at a more extreme level, disconnecting the catchment from the rest of the system. Given the extreme fragmentation of watersheds throughout the world (Zwick 1992; Dynesius and Nilsson 1994) and the growing evidence suggesting that anthropogenic disturbances can have strong effects at long distances from their source (Winston et al. 1991; Pringle 1997; Fausch et al. 2002), we suggest that our results may represent general phenomena in riverine systems, important for stream fishes and perhaps other aquatic species.

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Population dynamics of Japanese pink salmon (*Oncorhynchus gorbuscha*): are recent increases explained by hatchery programs or climatic variations?

Kentaro Morita, Shoko H. Morita, and Masa-aki Fukuwaka

Abstract: Hatchery programs involving the mass release of artificially propagated fishes have been implemented worldwide. However, few studies have assessed whether hatchery programs actually increase the net population growth of the target species after accounting for the effects of density dependence and climatic variation. We examined the combined effects of density dependence, climatic variation, and hatchery release on the population dynamics of Japanese pink salmon (*Oncorhynchus gorbuscha*) from 1969 to 2003. The population trends were more closely linked to climatic factors than to the intensity of the hatchery programs. The estimated contributions of hatchery-released fry to catches during the past decade are small. We concluded that the recent catch increases of Japanese pink salmon could be largely explained by climate change, with increased hatchery releases having little effect.

Résumé : On a utilisé partout dans le monde des programmes d'élevage qui comportent des libérations massives de poissons reproduits artificiellement. Peu d'études, cependant, ont évalué si ces programmes d'élevage augmentent de fait le taux net de croissance de population des espèces cibles, une fois qu'on a tenu compte des effets de la dépendance de la densité et de la variation climatique. Nous avons examiné les effets combinés de la dépendance de la densité, de la variation climatique et de la libération des poissons d'élevage sur la dynamique de population de saumons roses (*Oncorhynchus gorbuscha*) japonais entre 1969 et 2003. Les tendances démographiques sont liées plus intimement aux facteurs climatiques qu'à l'intensité des programmes d'élevage. Les contributions estimées des alevins provenant des élevages aux captures de pêche au cours de la dernière décennie sont limitées. Nous concluons que les augmentations récentes des captures de saumons roses japonais peuvent s'expliquer en grande partie par le changement climatique et que les libérations accrues de poissons d'élevage ont eu peu d'effet.

[Traduit par la Rédaction]

Introduction

In nature, climatic variation and density dependence are two of the most important factors regulating the population dynamics of fishes (e.g., Beamish and Bouillon 1993; Myers and Cadigan 1993). Artificial propagation is also becoming a major factor affecting the population dynamics of commercially important and endangered fishes. Hatchery programs that involve the mass release of artificially propagated fishes have been implemented worldwide to supplement wild populations and to increase fisheries harvests (Howell et al. 1999). The hatchery production of Pacific salmon is particularly copious, with approximately 5 billion salmon fry released annually (Mahnken et al. 1998). In Japan, catches of Pacific salmon increased during the last quarter of the 20th century, and hatchery release programs have been credited with this increase (Hiroi 1998; Kaeriyama 1999).

Although hatchery programs have been used as a major management tool, few studies have assessed whether hatchery programs actually increase net population growth of target species after accounting for the effects of density dependence and climatic variation (Hilborn 1999). Hilborn and Eggers (2000) indicated that there is little, if any, increase in total abundance of pink salmon (*Oncorhynchus gorbuscha*) owing to the hatchery program in Prince William Sound, Alaska, where more than 500 million fry are released annually, because catches from other areas in Alaska show equivalent increases. In contrast, Wertheimer et al. (2001) claimed that the net benefit from the hatchery program in Prince William Sound is substantial. In addition, adverse genetic and ecological effects of hatchery programs on the natural productivity of Pacific salmon have been suggested in recent years (e.g., Reisenbichler and Rubin 1999; Chilcote 2003; Nickelson 2003).

In this study, we examined the combined effects of density dependence, climatic variation, and hatchery release on the population dynamics of pink salmon around Hokkaido Island, Japan. Our results demonstrate that the recent increase in Japanese pink salmon catches can be largely ex-

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plained by climatic variation, with little contribution from increased hatchery releases.

Materials and methods

Study species

Pink salmon are the most abundant salmonids in the North Pacific Ocean, and their spawning rivers are distributed in the Pacific rim of Asia and North America at about 40°N (Heard 1991). Pink salmon have a unique 2-year life cycle. Breeding occurs in rivers during the fall, when fertilized eggs are buried in gravel in shallow water. After emerging from the gravel in spring, fry quickly descend to the sea. Pink salmon grow in the North Pacific Ocean, spend one winter at sea, and then return to their natal rivers to reproduce.

Several environmental factors that may affect the abundance of pink salmon have been suggested (reviewed by Heard 1991). In this study, we addressed the following four factors. First, temperature is one of the most important factors affecting survival (Smirnov 1947; Jaenicke et al. 1998; Su et al. 2004). In particular, several reports suggest that severe winters cause significant mortality among a variety of fishes including pink salmon (Smirnov 1947; Hurst and Conover 1998; Jaenicke et al. 1998). Second, low river discharge in the fall prevents adults from migrating upstream, decreases the available spawning area, and decreases oxygen concentration in the spawning redds; all of these factors combine to inhibit successful reproduction (reviewed by Wickett 1958). Third, large-scale climatic variability caused by the winter Aleutian low influences the productivity of Pacific salmon (Beamish and Bouillon 1993). Finally, density-dependent mortality during the egg stage has been suggested, because egg losses from superimposed redds are substantial (McNeil 1964; Fukushima et al. 1998). Additional factors such as predation and density dependence in the ocean have also been suggested to play an important role in survival (e.g., Willette et al. 1999), but these factors are not addressed here.

Data

We analyzed data on pink salmon from the coast of the Okhotsk Sea around Hokkaido Island (Fig. 1*a*, Okhotsk and Nemuro management regions) where most (99%) of the Japanese pink salmon catch occurs. We used data of commercial catches of pink salmon and the number of pink salmon fry released by hatcheries from 1969 to 2003 (Hokkaido Salmon Hatchery 1971–1998; National Salmon Resources Center 1999–2005). Pink salmon are caught by stationary traps from late July through early October, just before spawning, and are considered to be adults returning to adjacent rivers (~100 spawning rivers exist along the coast). In addition, pink salmon were collected from ~30 major rivers for hatchery broodstock, and fry were released in ~30 rivers and coastal waters.

We assumed that the annual commercial catch of pink salmon approximates real population changes over time for the following reasons. First, the fishing effort was relatively constant, with no trends between years (Souya, Abashiri, and Nemuro branch office areas in 1969–2003; chum salmon stationary trap, mean ± standard deviation (SD) = 312 ± 37, $r = 0.147$, $P = 0.414$; small stationary trap, 1652 ± 94, $r = 0.267$, $P = 0.120$; Ministry of Agriculture, Forestry, and Fisheries of Japan 1971–2005). Although the total number of stationary traps varied to some extent, we assumed that traps in good locations were operated each year. The annual catch was not correlated with the number of stationary traps (chum salmon stationary trap, $r = -0.189$, $P = 0.291$; small stationary trap, $r = 0.054$, $P = 0.759$). Second, the annual catch of pink salmon was correlated with other abundance indices. The annual catch was correlated with the total number of naturally spawning fish at Kunashiri Island (1991–2002, $r = 0.847$, $P < 0.001$; data from Kaev and Romasenko 2003) and with the total number of pink salmon caught in hatchery weirs (1969–2003, $r = 0.949$, $P < 0.001$; Hokkaido Salmon Hatchery 1971–1998; National Salmon Resources Center 1999–2005). Although the latter indicates that hatcheries took a constant proportion of returning adults, many adults were not used for broodstock because of hatchery capacity limitations and were not released (i.e., cost recovery). Therefore, it can be assumed that the pink salmon populations are subjected to a relatively constant harvest rate and that the annual catch is an indicator of the number of naturally spawning fish.

In addition, we used monthly mean air temperatures and total rainfall between September and October in Abashiri, as well as the winter Aleutian low pressure index (ALPI). The climatic data in Abashiri were obtained from the Japan Meteorological Agency (http://www.jma.go.jp). The ALPI was obtained from Fisheries and Oceans Canada (http://www.pac.dfo-mpo.gc.ca). Before the main analyses, we performed a standardized principal components analysis (PCA) of monthly temperatures during one generation of pink salmon. The first principal component was positively correlated with winter temperatures (Appendix A) and is hereafter referred to as the mild winter index (MWI). For PCA, we used temperature data obtained near the spawning grounds, which were positively correlated with sea surface temperatures in the North Pacific Ocean during winter (1970–2000; January, $r = 0.654$, $P < 0.001$; February, $r = 0.483$, $P = 0.006$; data from Japan Meteorological Agency 2001).

Population model

Two different models are commonly used to describe density-dependent population dynamics (Dennis and Taper 1994; Saitoh et al. 1999; Taper and Gogan 2002). The Gompertz population model assumes that density dependence is a log-linear function of abundance, whereas the Ricker population model assumes that density dependence is a linear function of abundance. Although fisheries scientists have typically used the Ricker population model, data of some recent studies on fishes, as well as our data, suggest that the Gompertz model is more appropriate (e.g., Bjørnstad et al. 1999; Hjermann et al. 2004). Here, we used the Gompertz population model incorporating climatic effects.

If the population is sustained solely by natural spawning, then the population model can be described by

$$(1)\quad N_t = N_{t-2}\exp(a + b\ln N_{t-2} + c_1\mathrm{MWI}_{t-2\text{ or }t} + c_2\mathrm{RF}_{t-2} + c_3\mathrm{ALPI}_{t-1})$$

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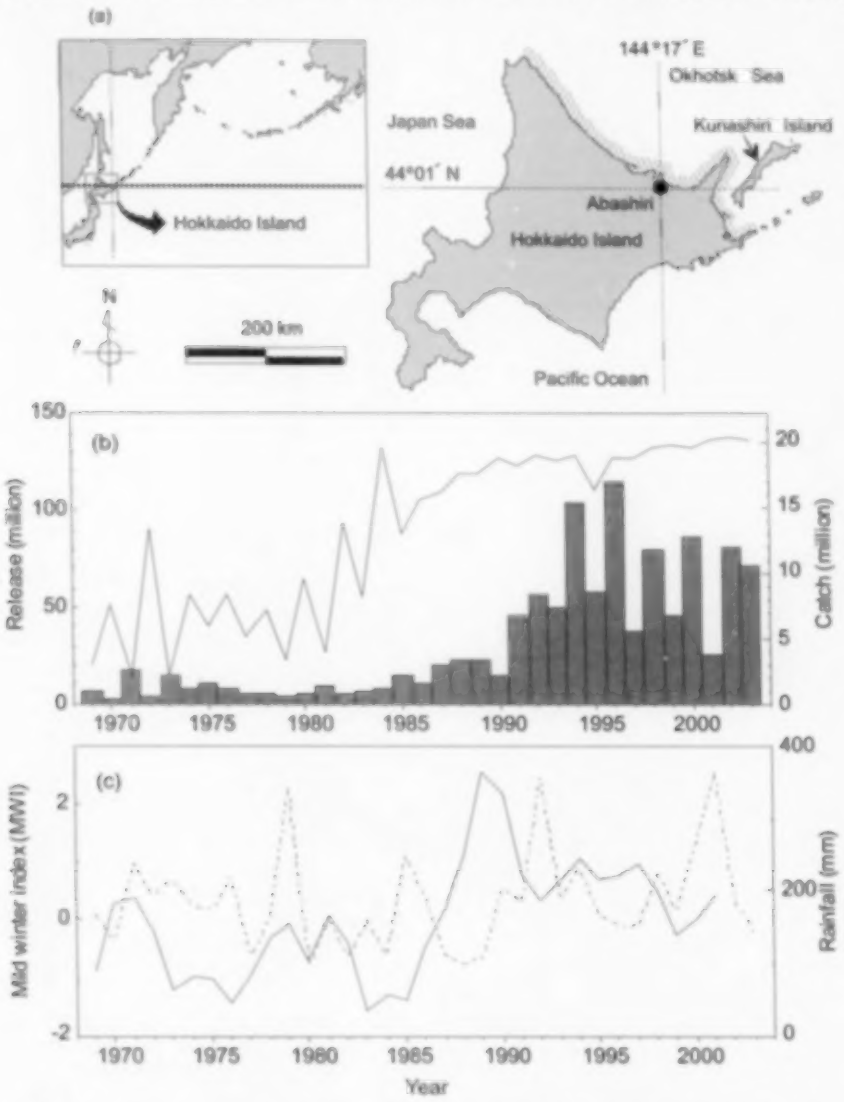
Fig. 1. (*a*) Location of the major fishing grounds for Japanese pink salmon (*Oncorhynchus gorbuscha*), i.e., Okhotsk and Nemuro management regions (stippled area) and the Abashiri meteorological observatory (solid symbol). (*b*) Long-term changes in pink salmon catches (bars) and number of fry released by hatcheries (line) in eastern Hokkaido, Japan, along the coast of the Okhotsk Sea. (*c*) Long-term changes in mild winter index (MWI; solid line) and total rainfall between September and October in Abashiri (broken line). MWI is the first principal component of monthly mean temperatures in Abashiri in the two years following a given year.



where N_t is the number of catches in year t, 2 denotes the generation time of pink salmon, $MWI_{t-2,t}$ is the mild winter index (i.e., first principal component of monthly temperatures during one generation of pink salmon), RF_{t-2} is the rainfall between September and October of the two previous years, and $ALPI_{t-1}$ is the ALPI of the previous year.

If the population is sustained solely by artificial propagation, then the population model can be described by

$$(2)\quad N_t = HR_{t-1}\exp(\alpha + \beta \ln HR_{t-1} + \gamma_1 MWI_{t-2,t} + \gamma_2 RF_{t-2} + \gamma_3 ALPI_{t-1})$$

where HR_{t-1} is the number of fry released in the previous year. Although RF_{t-2} was hypothesized to affect reproduction of naturally spawning fish (Wickett 1958), we used all climatic variables considered here to examine correlative relationships in addition to causal relationships.

More realistically, if the population is sustained by both natural spawning and artificial propagation, the population model can be described by

$$(3)\quad N_t = N_{t-2}\exp(a + b \ln N_{t-2} + c_1 MWI_{t-2,t} + c_2 RF_{t-2} + c_3 ALPI_{t-1}) + HR_{t-1}\exp(\alpha + \beta \ln HR_{t-1} + \gamma_1 MWI_{t-2,t} + \gamma_2 RF_{t-2} + \gamma_3 ALPI_{t-1})$$

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Table 1. Generalized R^2 and Schwarz information criteria (SIC) for the population models of Japanese pink salmon (*Oncorhynchus gorbuscha*).

Parental stock	Model	R^2	ΔSIC
Natural spawning	$N_t = N_{t-2}\exp(a)$	0.656	18.5
	$N_t = N_{t-2}\exp(a + b\ln N_{t-2})$	0.744	19.6
	$N_t = N_{t-2}\exp(a + c_1\mathrm{MWI}_{t-2-\tau} + c_2\mathrm{RF}_{t-2} + c_3\mathrm{ALPI}_{t-1})$	0.619	21.0
	$N_t = N_{t-2}\exp(a + b\ln N_{t-2} + c_1\mathrm{MWI}_{t-2-\tau} + c_2\mathrm{RF}_{t-2} + c_3\mathrm{ALPI}_{t-1})$	0.930	7.4
Hatchery	$N_t = \mathrm{HR}_{t-1}\exp(\alpha)$	0.234	37.8
	$N_t = \mathrm{HR}_{t-1}\exp(\alpha + \beta\ln \mathrm{HR}_{t-1})$	0.330	39.0
	$N_t = \mathrm{HR}_{t-1}\exp(\alpha + \gamma_1\mathrm{MWI}_{t-2-\tau} + \gamma_2\mathrm{RF}_{t-2} + \gamma_3\mathrm{ALPI}_{t-1})$	0.605	24.8
	$N_t = \mathrm{HR}_{t-1}\exp(\alpha + \beta\ln \mathrm{HR}_{t-1} + \gamma_1\mathrm{MWI}_{t-2-\tau} + \gamma_2\mathrm{RF}_{t-2} + \gamma_3\mathrm{ALPI}_{t-1})$	0.583	27.6
Natural spawning and hatchery	$N_t = N_{t-2}\exp(a) + \mathrm{HR}_{t-1}\exp(\alpha)$	0.748	15.2
	$N_t = N_{t-2}\exp(a + b\ln N_{t-2}) + \mathrm{HR}_{t-1}\exp(\alpha + \beta\ln \mathrm{HR}_{t-1})$	0.750	18.0
	$N_t = N_{t-2}\exp(a + c_1\mathrm{MWI}_{t-2-\tau} + c_2\mathrm{RF}_{t-2}) + \mathrm{HR}_{t-1}\exp(\alpha + \gamma_3\mathrm{ALPI}_{t-1})$	0.956	3.2
	$N_t = N_{t-2}\exp(a + b\ln N_{t-2} + c_1\mathrm{MWI}_{t-2-\tau} + c_2\mathrm{RF}_{t-2}) + \mathrm{HR}_{t-1}\exp(\alpha + \gamma_3\mathrm{ALPI}_{t-1})$	0.962	0.0

Note: SIC were measured relative to the best model. N_t, number of catches; HR, number of fry released by hatcheries; RF, rainfall in fall; MWI, mild winter index; ALPI, Aleutian low pressure index.

Here, "natural spawning" refers to fish spawning in the wild regardless of whether they originated from a hatchery or by natural spawning (cf. Goodman 2005). Although competition between hatchery fish and naturally spawned fish should occur to some extent in both rivers and coastal waters (Hilborn and Eggers 2000; Weber and Fausch 2003), it was not considered here. Because the population size of pink salmon is much smaller than that of chum salmon (*O. keta*; Kaeriyama 1999), the mass release of chum salmon fry (ca. 10-fold difference) is likely to mask the importance of competition among juvenile pink salmon.

The model parameters were estimated by the maximum likelihood method using the Solver maximization algorithms in Microsoft Excel®. We assumed a lognormal distribution of errors: $\ln(N_{obs}) = \ln(N_{est}) + \varepsilon$, where N_{obs} and N_{est} are the observed and estimated number of catches, respectively, and ε is the normal distribution of errors.

To compare the validity of several candidate models, we calculated the Schwarz information criterion (SIC) and generalized R^2 defined by Dennis and Otten (2000). The model with the lowest information criterion is the most parsimonious. In general, differences in information criterion >2 suggest that the models are statistically distinguishable. SIC has been suggested to be the appropriate information criterion for population models (Zeng et al. 1998; Dennis and Otten 2000; Taper and Gogan 2002). In addition, we used a likelihood ratio test to test each parameter.

Results

Both catches and hatchery releases of Japanese pink salmon increased dramatically over the last quarter of the 20th century except in the last decade (Fig. 1*b*). The number of fry released has been consistent at ~140 million per year since 1990 because of hatchery capacity limitations. Despite the constant number of fry released, the catch of pink salmon nonetheless fluctuated greatly. Within the last decade, the year-to-year differences have been as great as twofold. Even-numbered years dominated after 1994, while odd-numbered years dominated before 1975. The MWI showed a significant increasing trend during the time interval studied (Fig 1*c*; $r = 0.512$, $P = 0.002$). Most notable is the increase in MWI during the late 1980s. Rainfall and ALPI fluctuated from year to year, and neither showed any significant trend during the time interval studied (Fig. 1*c*; rainfall, $r = 0.106$, $P = 0.538$; ALPI, $r = 0.250$, $P = 0.153$).

The population models assuming naturally spawning fish as parental stock had larger generalized R^2 and smaller SIC than those assuming hatchery fish as parental stock, indicating that naturally spawned fish are the main contributors to catches (Table 1). The addition of climatic factors and density dependence for naturally spawning fish greatly improved the model. The model assuming both naturally spawning and hatchery fish as parental stock with specific combinations of climatic variations and density dependence for naturally spawning fish, i.e., $N_t = N_{t-2}\exp(a + b\ln N_{t-2} + c_1\mathrm{MWI} + c_2\mathrm{RF}) + \mathrm{HR}_{t-1}\exp(\alpha + \gamma_3\mathrm{ALPI})$, had the smallest SIC among all 288 possible models (Table 1, all results not shown) and was therefore the best of the models considered here. The best model suggests that survival of naturally spawned fish increases with increasing MWI, with increasing rainfall, and with decreasing population size ($b = -0.254$, $c_1 = 0.538$, $c_2 = 5.33 \times 10^{-3}$) and that survival of hatchery fish increases with increasing ALPI ($\gamma_3 = 1.120$). All parameters of the best model were statistically significant (likelihood ratio test, all $P < 0.01$). The predicted catches from the best population model corresponded well to observed catches (Fig. 2). The estimated contributions of hatchery fish to catches were 35.4% on average but only 17.5% during the past decade.

When we analyzed the data separately for odd- and even-numbered years, the importance of natural spawning tended to be obscured (Supplementary data, Tables S1–S3)[2]. The estimated contributions of hatchery fish to catches were in-

[2] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 4040. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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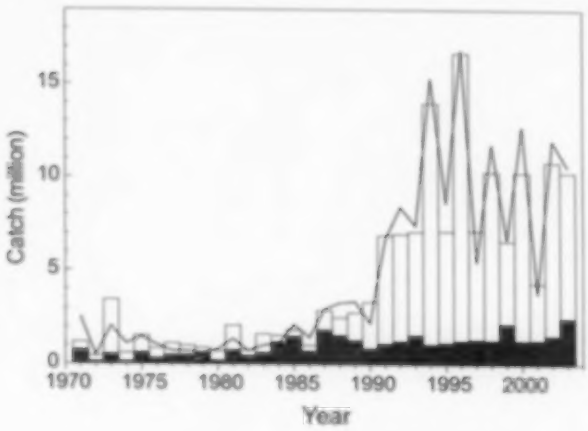
Fig. 2. Estimated catches of Japanese pink salmon (*Oncorhynchus gorbuscha*) that originated from natural spawning (solid bars) and hatcheries (open bars) using the best population model. The line indicates observed catches.



creased to 41.7% on average and to 22.6% during the past decade (Supplementary data, Fig. S1)[2]. However, the generality of the results did not change.

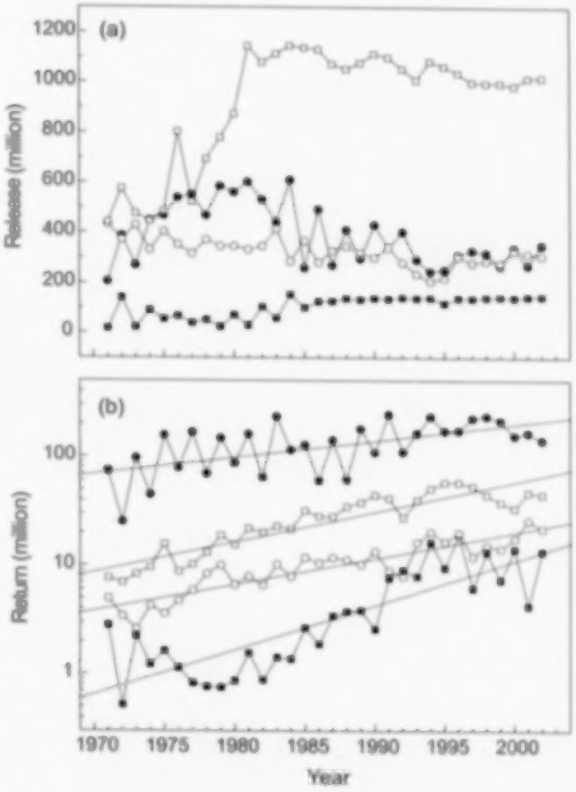
Discussion

The last quarter of the 20th century has seen a dramatic increase in the population size of Japanese pink salmon. This study demonstrated that the population dynamics of Japanese pink salmon are significantly influenced by density dependence, climatic variations, and the intensity of hatchery programs. However, the estimated contributions of hatchery fish to catches were not high during the past decade. No data are available in the literature to examine the observed contributions of hatchery fish to catches. Unexpectedly, our results did not suggest that the recent increases in pink salmon catches could be attributed to intensified hatchery programs; rather, the increases were attributed to climate change.

The increasing trends in both hatchery releases and catches in Japan could simply be a coincidental relationship between unrelated variables. This interpretation may be supported by evidence that Pacific salmon catches in some regions increased during the last quarter of the 20th century, irrespective of the level of artificial propagation (Beamish et al. 1997; Hilborn and Eggers 2000). The number of returning Pacific salmon also increased in Russia, even though the number of fry released was constant or reduced (Fig. 3). Remarkably, the number of returning chum salmon appears to be closely synchronized between Russia and Hokkaido, Japan (correlation of residuals against year, $r = 0.387$, $P = 0.029$). Although the number of returning pink salmon did not show such synchronization, it appears to be closely synchronized between Hokkaido and neighbouring Kunashiri Island, which has no hatcheries (Kaev and Romasenko 2003). Therefore, an environmental explanation for the recent increase in Japanese salmon catches may be more reasonable than an explanation invoking artificial propagation.

Our estimates regarding the contribution of naturally spawned pink salmon to catches were very large compared

Fig. 3. (*a*) Long-term changes in the number of chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) fry released by hatcheries on Hokkaido Island, Japan (chum, open squares; pink, solid squares), and in Russia (chum, open circles; pink, solid circles). (*b*) Long-term changes in the number of chum and pink salmon returning to Hokkaido (chum, open squares; pink, solid squares) and Russia (chum, open circles; pink, solid circles). Hokkaido returns include coastal commercial catch and hatchery river catch. Hokkaido data are from the website of the National Salmon Resources Center (http://www.salmon.affrc.go.jp/) and this study. Russian returns include commercial catch and escapement of adult to spawning area. Russian data are from Eggers et al. (2003), North Pacific Anadromous Fish Commission (2003), Pacific Research Fisheries Centre (2001, 2002, 2003), and unpublished data (Working Group on Stock Assessment, North Pacific Anadromous Fish Commission, Suite 502, 889 West Pender Street, Vancouver, BC V6C 3B2, Canada). Regressions: Russian pink, $\ln(y) = 0.0353x - 51.4$, $r = 0.607$, $P < 0.001$; Russian chum, $\ln(y) = 0.0553x - 93.7$, $r = 0.899$, $P < 0.001$; Hokkaido pink, $\ln(y) = 0.0941x - 172$, $r = 0.836$, $P < 0.001$; Hokkaido chum, $\ln(y) = 0.0634x - 109$, $r = 0.915$, $P < 0.001$.



with pervasive beliefs (Augerot 2005; Hiroi 1998; Kaeriyama 1999) and may have been overestimates. However, it is possible that the contribution of natural spawning to catches was large for the following three reasons. First, the pink salmon catch showed a biennial oscillation, even though the number of fry released was constant. Because pink salmon have a fixed 2-year life cycle, this oscillation indicates a substantial contribution of wild fish. Second, the

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population trends were closely linked to climatic variables related to the reproduction of naturally spawning pink salmon (i.e., rainfall in the fall of the two previous years; Wickett 1958). Third, the recapture rates of thermally marked pink salmon were very low (percentage of fry marked upon release in 2001, Tokushibetsu River = 42%, Ichani River = 62%; percentage of adults marked upon their return in 2002, Tokushibetsu River = 1%, Ichani River = 4%; data from the National Salmon Resources Center 2004). Because the straying rate of pink salmon is believed to be high compared with that of other salmonids (~1%–35%; reviewed by Altukhov et al. 2000; Hendry et al. 2004) and because most hatcheries do not conduct thermal marking, it is difficult to estimate the contribution of hatchery fish based on limited marking data. However, the extremely low recapture rate of marked fish suggests a low survival rate of hatchery fish. In Japan, the early summer run has been selectively used for broodstock to separate run timing of pink salmon from that of chum salmon, which may have an adverse effect on the survival of hatchery-reared pink salmon.

The patterns of covariation between climatic variables and the population growth of pink salmon are consistent with those of previous studies (e.g., Wickett 1958; Beamish and Bouillon 1993; Jaenicke et al. 1998). The population growth of pink salmon was significantly enhanced by mild winters, high rainfall during fall, and an intensified winter Aleutian low. Empirical studies have indicated the following: mild winters prevent spawning grounds from freezing, which in turn decreases egg mortality (Smirnov 1947); high rainfall increases river discharge, which in turn enhances the upstream migration of adults, increases the available spawning area, and increases oxygen concentration (Wickett 1958); and an intensified Aleutian low can enhance upwelling and turbulence, which in turn increases the abundance of zooplankton (Beamish and Bouillon 1993). Although Japanese pink salmon are distributed near the southern limits of their natural range, a severe winter could still cause the freezing of spawning grounds, because average winter temperatures (January to February) in Abashiri ranged from −10.4 to −3.5 °C during the study periods. In addition, winter warming would also decrease winter mortality in the ocean. Several reports have suggested that severe winters cause major mortality among a variety of fishes (e.g., Hurst and Conover 1998).

The following is an overview of our deductions pertaining to the recent trends in the population dynamics of Japanese pink salmon. Remarkable increases in abundance occurred in the 1989 odd and 1990 even year classes because of very warm winters for both year classes. Further increases in abundance occurred in the 1992 even year class because of very high rainfall during the fall of 1992, and even-numbered years dominated after 1994. Similarly, a further increase in abundance occurred in the 2001 odd year class because of very high rainfall during the fall of 2001. Winters have been relatively warm and population size has been historically high over the past decade.

Management implications

The recent increase in catches of Japanese pink salmon can be largely explained by climate variation, with little contribution from hatchery release. Our findings do not support the pervasive belief that intensified hatchery programs have resulted in the observed increase in the abundance of pink salmon. The effectiveness of hatchery programs should therefore be reconsidered. Because it is important to protect genetic diversity and the viability of natural populations, any hatchery programs intended to maintain harvest rates during poor environmental conditions should take into account the impacts, particularly from mixed-stock fisheries, on natural populations already struggling under difficult climatic conditions. In addition to hatchery programs, alternative management tools should be implemented more actively, including spawning-bed enhancement, removal of dams, and improvement of fish passage (Bednarek 2001; Merz et al. 2004; Sagawa et al. 2004). Such conservation management tools will guarantee the long-term sustainability of salmon stocks.

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(Appendix A follows.)

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Appendix A

Table A1. Correlation coefficients between the first principal component (PC1) and monthly mean air temperatures in Abashiri during one generation of pink salmon (*Oncorhynchus gorbuscha*) returning in year t (*, $p < 0.05$; **, $p < 0.01$).

Year	Month	PC1
$t-2$	September	0.240
	October	0.597**
	November	0.487**
	December	0.499**
$t-1$	January	0.523**
	February	0.598**
	March	0.691**
	April	0.252
	May	0.231
	June	0.061
	July	−0.038
	August	−0.071
	September	0.205
	October	0.698**
	November	0.558**
	December	0.513**
t	January	0.677**
	February	0.484**
	March	0.375*
	April	0.173
	May	0.142
	June	0.079
	July	−0.029
	August	−0.078

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Have brook trout (*Salvelinus fontinalis*) displaced bull trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams?

Bruce E. Rieman, James T. Peterson, and Deborah L. Myers

Abstract: Invasions of non-native brook trout (*Salvelinus fontinalis*) have the potential for upstream displacement or elimination of bull trout (*Salvelinus confluentus*) and other native species already threatened by habitat loss. We summarized the distribution and number of bull trout in samples from 12 streams with and without brook trout in central Idaho and used hierarchical regression analysis to consider whether brook trout have displaced bull trout along gradients of temperature and elevation. Brook trout generally were observed in higher numbers downstream of bull trout. Brook trout presence, number, and both temperature and elevation were important variables explaining the observed distributions and number of bull trout among streams. Our analyses support the hypothesis that brook trout have displaced bull trout, but results were highly variable and stream dependent. Although brook trout appeared to have displaced bull trout to higher elevations or colder temperatures, there was no clear influence on overall number of bull trout. Brook trout probably do influence bull trout populations and facilitate if not cause local extinctions, but threats probably vary strongly with environmental conditions. Bull trout in smaller streams could be more vulnerable than those in larger streams.

Résumé : Les invasions d'ombles de fontaine (*Salvelinus fontinalis*) non indigènes peuvent potentiellement déplacer vers l'amont ou éliminer les ombles à tête plate (*Salvelinus confluentus*) ou d'autres espèces indigènes déjà menacées par les pertes d'habitat. Nous avons compilé la répartition et l'abondance des ombles à tête plate dans des échantillons provenant de 12 cours d'eau avec ou sans ombles de fontaine dans le centre de l'Idaho; nous avons utilisé l'analyse de régression hiérarchique afin de voir si l'omble de fontaine a déplacé l'omble à tête plate le long de gradients de température et d'altitude. L'omble de fontaine se retrouve et s'observe généralement en plus grand nombre en aval de l'omble à tête plate. La présence et le nombre d'ombles de fontaine, ainsi que la température et l'altitude, sont des variables explicatives des répartitions observées et des nombres d'ombles à tête plate dans ces cours d'eau. Nos analyses appuient l'hypothèse qui veut que l'omble de fontaine déplace l'omble à tête plate, mais les résultats sont très variables et ils changent d'un cours d'eau à un autre. Bien que l'omble de fontaine semble avoir déplacé l'omble à tête plate vers les altitudes plus élevées ou les températures plus froides, il n'y a pas d'influence claire sur les nombres totaux d'ombles à tête plate. L'omble de fontaine influence vraisemblablement les populations d'ombles à tête plate et facilite, sans nécessairement les causer, des extinctions locales; le danger varie cependant fortement d'après les conditions du milieu. Il se peut que les ombles à tête plate des plus petits cours d'eau soient plus menacés que ceux des cours d'eau plus grands.

[Traduit par la Rédaction]

Introduction

Distributions of ecologically similar fishes within individual rivers or streams are sometimes complementary (e.g., Quist et al. 2004). Two native chars (*Salvelinus leucomanis*, *Salvelinus malma*) found in Japan, for example, are distributed differently along distinctive altitudinal or thermal gradients (Fausch et al. 1994; Nakano et al. 1996; Taniguchi and Nakano 2000). Although distributions may overlap, one species (*S. leucomanis*) predictably occurs in allopatry in warmer downstream water, with the other (*S. malma*) upstream in colder water. Similar patterns have been observed with an introduced char, brook trout, and either native cutthroat trout (*Oncorhynchus clarkii*) (Fausch 1989; Dunham et al. 1999, 2002*a*) or bull trout (Paul and Post 2001; Gunckel et al. 2002) in the western US and Canada. Brook

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trout are typically found downstream of, and overlapping with, the native forms unless they are introduced to a headwater lake that essentially reverses the thermal gradient and direction of invasion from that in streams without lakes (Adams et al. 2001).

Maintenance of distinctive distributions may result from important differences in behavior and physiological responses controlling individual species habitat use and (or) their interactions along thermal gradients (Fausch 1989; Taniguchi et al. 1998; Dunham et al. 2002*a*). For native species that have coexisted within individual watersheds for thousands of years, selective segregation could minimize overlap. In the case of introduced and native species such as brook trout and cutthroat or bull trout, direct interaction could be more likely and could have important implications for conservation management (Dunham et al. 2002*a*).

Some believe that brook trout (and other introduced species) are one of the primary causes of decline in cutthroat trout (Young 1995; and see Dunham et al. 2002*a* for a review) and bull trout (Rieman and McIntyre 1993; Rieman et al. 1997) throughout the range of the latter two species. Anecdotal evidence of a widespread loss of native species precipitated by brook trout seems strong. Brook trout now occur in most of the US Geological Survey 5th code (~15 000 ha) watersheds of the interior Columbia River basin (Lee et al. 1997). Managers throughout the region have experimented with brook trout removal and installation of in-stream barriers in hopes of stemming the invasion (Kruse et al. 2001; Dunham et al. 2002*a*; Novinger and Rahel 2003).

The empirical evidence is less clear. Leary et al. (1993) demonstrated a progressive shift in numerical dominance from bull trout to brook trout at sampling sites in the zone of sympatry in Lolo Creek, Montana, but a population-level effect could not be discerned. Others have found evidence of direct interaction between brook trout and native species (Peterson et al. 2004*a*; Gunckel et al. 2002), but the results are variable (Dunham et al. 1999; Rich et al. 2003) and some invasions appeared to be stalled (Adams et al. 2002). From our own work (B.E. Rieman, unpublished data) and that of others, it appears that co-occurrence of brook trout and native salmonids within individual streams may be common (Adams 1994, 1999; Dambacher and Jones 1994). Although co-occurrence does not imply indefinite coexistence, it does suggest elimination of native forms is not inevitable throughout the range of streams accessible to brook trout (Dunham et al. 2002*a*).

Taniguchi and Nakano (2000), Fausch et al. (1994), and others have shown that the interactions of species may be strongly conditioned by temperature, which produces predictable patterns of occurrence along thermal gradients. The nature of those interactions, however, may be complex (Fausch 1989; Fausch et al. 1994), producing variation in patterns across distinctive environments. A full understanding of the processes and complexity involved will undoubtedly require carefully designed, manipulative experiments (e.g., Taniguchi and Nakano 2000; Peterson and Fausch 2003; Peterson et al. 2004*a*). A better documentation of patterns that exist in current distributions, however, can provide important clues about the generality and scale of interactions between species not possible with typical manipulative experiments focused on habitat-unit or even stream-reach scales. If a strong interaction and displacement are important, we anticipate that elevation or thermal distribution limits of a native species will differ in the presence or absence of the introduced form.

In this work, we focused on patterns of occurrence of bull trout and their co-occurrence with brook trout. Bull trout is a species of particular concern in the northwestern United States (Rieman et al. 1997) and is currently listed as a threatened species under the US Endangered Species Act. The natural distribution of bull trout includes much of the northwestern US and Canada (Haas and McPhail 1991). Bull trout may express a variety of life history patterns, but in general, juveniles rear in natal or nearby streams for at least 1–3 years. Subsequently, some fish may migrate to a downstream river or lake and return to the natal stream to spawn for the first time at 5–7 years of age (Rieman and McIntyre 1993). Other resident fish may remain in the natal streams throughout life (Rieman and McIntyre 1993). Both life histories appear to be common throughout the range. In central Idaho, migratory fish may be found virtually anywhere in the large river systems they inhabit, but spawning adults and juvenile fish, as well as residents of all ages, occur almost exclusively in higher elevation, colder, headwater streams (Dunham and Rieman 1999; Dunham et al. 2003). Selong et al. (2001) have shown that temperatures associated with optimum growth efficiency of bull trout are lower than those for other salmonids of the region, including brook trout.

Brook trout have been widely established by introduction and subsequent invasion throughout the region beginning before 1900; they are now one of the most widely distributed species within the interior Columbia River basin (Lee et al. 1997). There has been relatively little work describing the life history of brook trout in the region, but they can mature much earlier (2–3 years of age; Adams 1999; Kennedy et al. 2003) than bull trout. Brook trout have been associated with low gradient streams and commonly have been found inhabiting lower elevations of streams occupied by other native salmonids (Adams 1999; Dunham et al. 1999; Paul and Post 2001). Adams (1999) demonstrated that stream gradient and swimming ability did not limit upstream distributions, but declining growth associated with reduced temperature could produce a demographic constraint to an upstream invasion. Nakano et al. (1998) and Gunckel et al. (2002) demonstrated that competition may be important between brook trout and bull trout, and Adams (1994) provided some evidence that an upstream displacement of the lower limit of bull trout distribution may occur in the presence of brook trout. Hybridization between brook trout and bull trout also has been widely documented where the two species overlap (Markle 1992; Leary et al. 1993; Kanda 1998). It appears that hybrids may be sterile or experience low survival (Leary et al. 1993; Kanda 1998). If brook trout mature earlier or occur at higher densities than bull trout, they could ultimately displace bull trout through a reproductive advantage (Leary et al. 1993).

Even if brook trout do not entirely displace bull trout, they could push the populations into more and more restricted distributions in headwater streams. Because smaller and more isolated bull trout populations are vulnerable to local extinction through other causes (Dunham and Rieman 1999),

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even incomplete upstream displacement by brook trout could seriously threaten remnant bull trout populations.

To consider whether brook trout have had an important effect in streams of central Idaho, we used regression analysis to describe the occurrence and number of bull trout along elevation and thermal gradients in streams with and without brook trout. We hypothesized that bull trout would occur in strong association with either temperature or elevation, but that distribution and density would be altered in the presence of, or at higher densities of, brook trout. Conceivably, brook trout might simply replace (rather than displace) bull trout as bull trout distributions or numbers contract because of other causes such as habitat degradation. If that were the case, we would anticipate no consistent brook trout effect in the analysis. We predicted that if brook trout do displace bull trout, brook trout would either be associated with (*i*) a reduction in overall density or probability of occurrence of bull trout evidenced by a negative effect in the analysis or (*ii*) upstream displacement of fish, evidenced as an interaction effect (i.e., the relationship with temperature or elevation would change with brook trout).

Materials and methods

Study streams

Bull trout and brook trout occur in tributary streams of several of the larger river basins in south central Idaho. We selected streams that spanned the elevation range encompassing the lower limits of bull trout distributions observed in other work (Dunham and Rieman 1999) that were small enough to sample effectively by snorkeling and backpack electrofisher and that had no headwater lakes that might support a downstream rather than upstream invasion of brook trout. We chose streams known from recent sampling to support both brook trout and bull trout or bull trout alone. Other species that occurred at least occasionally included rainbow trout (*Oncorhynchus mykiss*), sculpin (*Cottus* spp.), and Chinook salmon (*Oncorhynchus tshawytscha*), all native forms. Because we could not find enough streams fitting our criteria within a single river basin, we selected streams distributed across three neighboring river basins (Fig. 1). All streams were located in mountainous terrain and predominantly forested watersheds. All streams were located in geologies of igneous and metamorphic origin with low conductance (<120 μS). Average annual precipitation across sites has been ~40 cm, predominantly as snow. Study streams were small (mean width 3.8–9.2 m at summer low flow), cold (summer mean temperatures <12.4 °C), and supported modest amounts of large woody debris (~1–6 pieces·100 m^{-2}) (Table 1). Observed densities of small bull trout among streams and sites varied by more than an order of magnitude; observed brook trout densities were more consistent where brook trout occurred (Table 1).

Field sampling

Our general approach was to distribute sampling sites throughout each study stream over the elevation ranges bounding the lower limits of the bull trout distribution. Sampling in 1996 was conducted as a pilot study to identify the general bounds of the species distributions and to insure that both species were either present or absent in the proposed study streams as anticipated. We sampled 14 streams in 1996. In 1997, we dropped two streams from further consideration: one because of recent disruptive land use and the other because of logistical constraints. In 12 streams (five bull and brook trout; seven bull trout only) included in our final analysis, we sampled 11–31 sites above and below the anticipated lower bound of the bull trout distribution in each stream. We distributed sample sites to insure longitudinal representation, but access to some stream reaches was not possible. The number and distribution of sites ultimately sampled in each stream was a function of both systematic and logistic constraints. Sampling was conducted in late summer when streams were at or near base flow to minimize changes in channel characteristics and maximize sampling effectiveness.

Our sampling encompassed a minimum of 12 m of stream at each site. The distance sampled was varied to ensure that at least two pools (believed to be preferred habitat for bull trout) were included in each site; length of all sites averaged about 36 m. In 1996, we used snorkeling or electrofishing to sample fish at each site. Snorkeling was conducted during the day following the procedures established by Thurow (1994). In 1997, sampling was conducted exclusively by electrofishing following the procedures outlined by Rieman and McIntyre (1995). We used electrofishing for the final collection methods because detection efficiencies for daytime snorkeling are generally lower than those for electrofishing (Peterson et al. 2002) and because snorkelers were not confident in their discrimination between brook trout and bull trout that were not encountered at close range. The two species have similar coloration and markings and may be confused at a distance. We classified the two species based on presence (brook trout or hybrid) or absence (bull trout) of pigmentation in the dorsal fin and vermiculations on the back. Discrimination of the two species "in hand" can be highly accurate, although hybrids may be problematic (Adams 1994). To verify our classifications, we collected fin tissues from all putative bull trout, brook trout, or hybrids sampled in the field and submitted a blind sample for genetic analysis as described by Spruell et al. (2001) for confirmation. Field classification was accurate for species (i.e., no fish visually classified as bull trout were really brook trout and vice versa; Table 2), although hybrids were less clear. We limited our analysis to fish classified either as bull trout or brook trout and excluded hybrids from our analysis.

Total length was recorded for every fish sampled. We summarized numbers of bull trout observed as a density with the total number of bull trout smaller than 150 mm divided by area sampled. We summarized the number of all brook trout in a similar fashion. We limited our analysis to small bull trout because they are most closely associated with the elevation and thermal gradients that appear to define the extent of suitable natal environments or patches (Dunham and Rieman 1999; Dunham et al. 2002*b*). We also assumed that small fish are more likely to interact directly with brook trout or to represent the outcome of any past interaction between adults. We did not correct our samples for incomplete or variable detection probabilities of either species, so there is the possibility of some bias in our estimates relative to the true number of fish present in each sample site. However, preliminary studies indicated that electrofishing capture effi-

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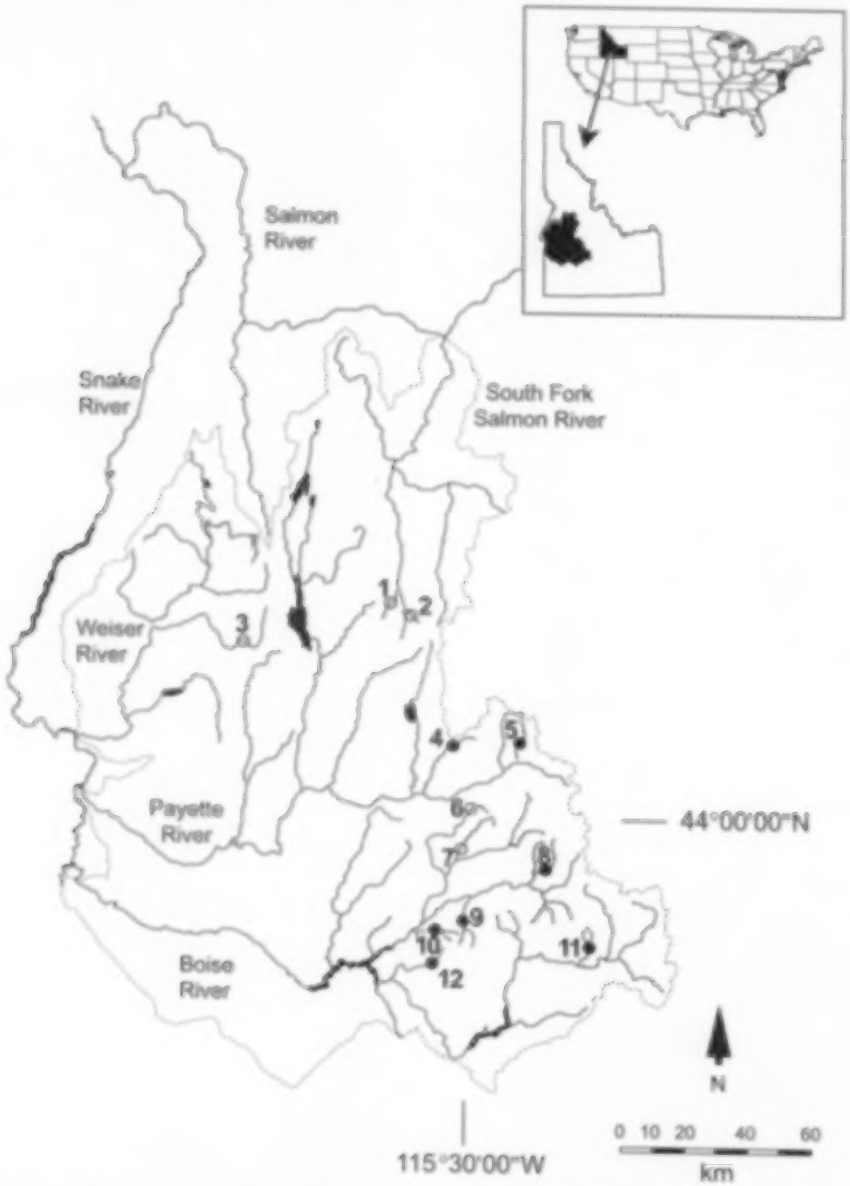
Fig. 1. Study streams located in central Idaho, USA: (1) Trail Creek, (2) Lodgepole Creek, (3) Little Weiser River, (4) Clear Creek, (5) Canyon Creek, (6) Crooked River, (7) Bear River, (8) Queens River, (9) Roaring River, (10) Sheep Creek, (11) Skeleton Creek, (12) Rattlesnake Creek. Open and solid circles represent streams with brook trout (*Salvelinus fontinalis*) present and absent, respectively. The dotted line outlines watershed boundaries depicted by the inset.



ciencies were similar and averaged 14.6% and 16.3% for brook trout and bull trout, respectively (J.T. Peterson, unpublished data).

At each site, we recorded the elevation and two channel characteristics, mean wetted width and density of large wood, that have been commonly associated with the distribution or number of bull trout (Dambacher and Jones 1997; Dunham and Rieman 1999; Rich et al. 2003). Elevation was recorded from standard topographic maps. Wetted width was measured at the top, bottom, and approximate midpoint of each sample site and averaged. All large wood (>10 cm diameter; >3 m length) within or above the wetted channel was counted and summarized as total pieces divided by area sampled.

Thermographs were installed in each stream at three to seven sites. One thermograph was placed near the highest and lowest sample sites, and others were distributed between those two. Temperatures were recorded at 4 h intervals and summarized to a single mean for the period between 15 July and 31 August, an interval roughly symmetric about the

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Table 1. The number of sampling sites (*N*), mean, and standard error (in parenthesis) of selected characteristics for the 12 study streams in central Idaho.

Stream	*N*	Elevation (m)	Average stream temperature (°C)	Mean wetted width (m)	Wood density (no.·100 m^{-2})	Small[a] bull trout (*Salvelinus confluentus*) density (no.·100 m^{-2})	Brook trout (*Salvelinus fontinalis*) density (no.·100 m^{-2})
Bear River	12	1562 (210)	10.85 (0.22)	6.41 (0.39)	1.49 (0.36)	0.36 (0.23)	0.50 (0.17)
Canyon Creek	14	1829 (380)	8.85 (0.03)	5.73 (0.67)	2.30 (0.76)	2.77 (0.60)	0
Clear Creek	30	1943 (150)	7.97 (0.11)	5.32 (0.30)	2.99 (0.25)	0.44 (0.12)	0
Crooked River	20	1813 (420)	9.28 (0.40)	6.61 (0.51)	1.44 (0.28)	0.73 (0.31)	0.40 (0.19)
Lodgepole Creek	16	1715 (150)	9.04 (0.16)	3.78 (0.22)	5.70 (1.00)	2.10 (0.53)	0.51 (0.28)
Little Weiser River	19	1577 (420)	11.41 (0.23)	5.34 (0.33)	0.91 (0.19)	0.54 (0.25)	0.16 (0.09)
Queens River	17	1699 (220)	9.55 (0.09)	9.16 (0.52)	1.51 (0.28)	0.17 (0.12)	0
Roaring River	15	1544 (340)	11.09 (0.26)	7.66 (0.24)	1.62 (0.56)	0.28 (0.14)	0
Rattlesnake Creek	20	1507 (340)	12.35 (0.33)	4.63 (0.15)	5.43 (1.03)	0.61 (0.25)	0
Sheep Creek	18	1507 (210)	11.60 (0.20)	5.49 (0.25)	2.22 (0.66)	0.13 (0.09)	0
Skeleton Creek	19	1892 (460)	9.49 (0.22)	4.95 (0.30)	4.53 (0.97)	1.55 (0.53)	0
Trail Creek	13	1678 (270)	10.21 (0.20)	5.34 (0.72)	5.10 (1.19)	1.16 (0.43)	0.18 (0.13)

[a]<150 mm.

Table 2. Cross classification of brook trout (*Salvelinus fontinalis*), bull trout (*Salvelinus confluentus*), and brook trout × bull trout hybrids identified by visual observation in the field and by genetic analysis to detect pure and hybrid fish.

	True class (genetic)		
Field class (visual)	Bull trout	Brook trout	Hybrid
Bull trout	33	0	2
Brook trout	0	17	3
Hybrid	1	0	25

warmest period in these streams. We estimated the mean temperature for each sample site by linear interpolation.

Statistical analysis

We were primarily interested in the association of bull trout density and occurrence along gradients of temperature and elevation with varied occurrence and density of brook trout. We included wood density and mean stream width as "nuisance" variables in the analysis because they have also been associated with the density and detection of bull trout in streams and could confound the analysis if not accounted for in the models (Peterson et al. 2004*b*).

We conducted analyses with both estimated temperature and elevation for each sample site. Elevation is strongly correlated with temperature in these data, and we assumed that the influence of temperature was the primary mechanism explaining any patterns that emerged in association with either variable. Because we estimated temperature through interpolation, an error was introduced into the independent variable. Temperature estimates were not possible for sites outside the thermograph distribution, and thermograph failures also reduced the number of observations, so the analyses with temperature were more limited than those based on elevation. We contrasted the associations of temperature and elevation to provide the best model to evaluate brook trout effects, but we did not consider temperature or elevation simultaneously in any of the candidate models, with exception of the global model.

We considered both density and occurrence (presence–absence) of bull trout observed in our samples in separate analyses. Density may provide more information, but patterns of occurrence for locally rare or low-density species like bull trout may carry almost as much information (Royle and Nichols 2003) and often can be collected with lower cost. Absence also carries a different implication than low numbers from a conservation perspective (i.e., local extirpation vs. decline). We wanted to contrast the analyses to consider their consistency and the utility of alternative sampling approaches in future work.

We summarized data graphically to display general patterns along elevational gradients in streams with and without brook trout. We were concerned that observations within streams could be spatially autocorrelated, which would preclude the use of traditional regression techniques (Sokal and Rohlf 1995). Thus, we initially fit a global (i.e., all predictors) linear and logistic regression model of bull trout density and presence, respectively. An analysis of variance of the residuals from each global model indicated significant spatial autocorrelation for linear ($F = 5.510$; df = 11, 198; $P < 0.001$) and logistic ($F = 2.891$; df = 11, 198; $P = 0.002$) regression models. To account for the spatial autocorrelation, we examined relationships among sample site characteristics (Table 1) with hierarchical models. Hierarchical models differ from more familiar regression techniques in that autocorrelation among sample sites within streams, defined as lower level units (sample sites) within upper level units (streams), is incorporated by including random effects for lower level intercepts and slopes (Snijders and Bosker 1999). For our study, random effects are estimates of the variability of the effect of site-specific (lower level unit) characteristics on bull trout density and presence among streams (upper level units). For example, a stream temperature random effect estimates the extent to which the relationship between stream temperature and bull trout presence (i.e., the regression slope) varies from stream to stream. Fixed effects are estimates of the average effect of site-specific characteristics across streams and the effect of stream-level characteristics (e.g., mean brook trout density; Table 1) on bull trout density and presence.

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Table 3. Biological interpretation of predictors used in candidate models relating the local and watershed-level factors influencing bull trout (*Salvelinus confluentus*) density and presence.

Predictor variables	Biological interpretation (hypothesis)
Elevation	Longitudinal position and local climate effects; potential surrogate for stream temperature
Mean temperature	Mean summer water temperature influencing behavior and physiology
Mean width, wood density	Channel characteristics influencing cover and the amount and capacity of local habitats
Mean brook trout (*Salvelinus fontinalis*) density	Direct interaction influencing density or occurrence through aggression, competition, or predation throughout the stream
Elevation × mean brook trout density	Direct interaction influencing bull trout density or occurrence through aggression, competition, or predation mediated by elevation
Mean temperature × mean brook trout density	Direct interaction influencing density or occurrence through aggression, competition, or predation mediated by temperature gradients

Prior to model selection, we evaluated goodness-of-fit for each candidate model by examining (*i*) normal probability plots of the lower (site) level residuals and (*ii*) plots of the empirical Bayes residuals by their corresponding χ^2 scores with $Q - 1$ degrees of freedom, where Q is the number of upper (stream) level effects included in the candidate model (Bryk and Raudenbush 1992).

We used the information-theoretic approach, described by Burnham and Anderson (2002), to evaluate the relative plausibility of models relating sample site and stream characteristics to bull trout density and occurrence. For each response, we constructed a global model with all predictors (Table 3). From the global model, we constructed a subset of 15 candidate models. Six were based on temperature and six on elevation. Our primary hypotheses of interest reflected the influence of brook trout on the distribution or density of bull trout, so we first contrasted models with and without brook trout effects. A model with a brook trout interaction (brook trout × elevation; brook trout × temperature) always included the main effect (brook trout and elevation or temperature). We also contrasted models that systematically excluded temperature, elevation, and width and wood density to determine whether these variables were actually useful in explaining variability among sites and streams as anticipated. As explained above, width and wood density were not evaluated independently.

To assess the relative fit of each candidate model, we calculated Akaike's Information Criterion (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989). AIC is an entropy-based measure used to compare candidate models for the same data (Burnham and Anderson 2002), with the best-fitting model having the lowest AIC_c. The number of parameters used to estimate AIC_c included the fixed effects, random effects, and random effect covariances when two or more random effects were included in the candidate model (Burnham and Anderson 2002). The relative plausibility of each candidate model (i.e., hypothesis) was assessed by calculating Akaike weights as described in Burnham and Anderson (2002). These weights can range from 0 to 1, with the most plausible candidate model having the highest weight.

Model averaging, as a means of incorporating model selection uncertainty into parameter estimates, is not appropriate for models consisting of fixed and random effects (K. Burnham, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA, personal communication). Therefore, instead of basing our inferences and predictions on a single best model, we report estimates of fixed and random effects for our confidence set of hierarchical linear and logistic models, as determined by the Akaike weights. A confidence set of models is analogous to a confidence interval for a parameter estimate and is a useful means of assessing model selection uncertainty (Burnham and Anderson 2002). Because the ratio of Akaike

Fig. 2. Stream width and (*a*) elevation or (*b*) estimated mean August temperature associated with the lowest observations of bull trout (*Salvelinus confluentus*) in 14 study streams with brook trout (*Salvelinus fontinalis*) present (open circles) or absent (solid circles) sampled by snorkeling and electrofishing in 1996.

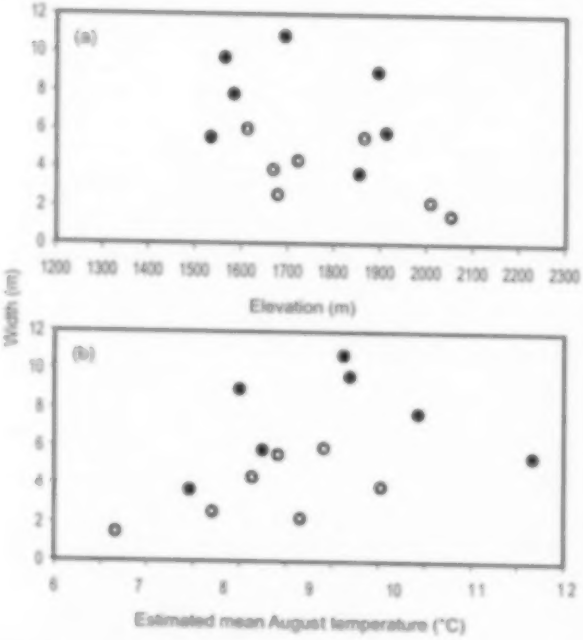

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Fig. 3. Observed densities of bull trout (*Salvelinus confluentus*) (solid circles) and brook trout (*Salvelinus fontinalis*) (open circles) and estimated mean August temperature (*) by elevation in 12 study streams sampled by electrofishing 1997.

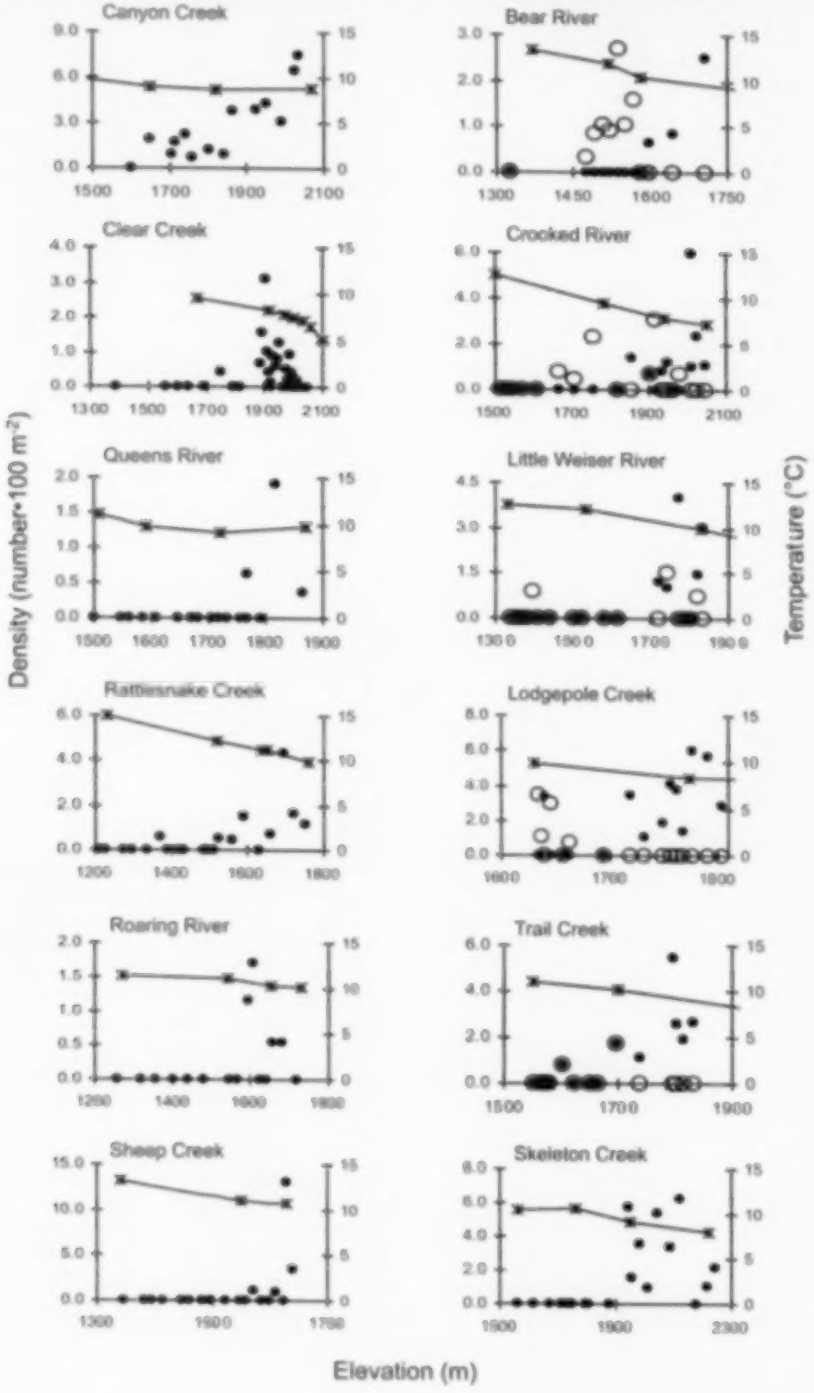

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Table 4. Predictor variables, number of parameters (K), log-likelihood (Log$L$), Akaike's Information Criterion with the small-sample bias adjustment (AIC_c), ΔAIC_c, and Akaike weights (w) for the set of candidate models (i) for predicting bull trout (*Salvelinus confluentus*) density.

Candidate model	K	Log$L$	AIC_c	ΔAIC_c	w_i
Elevation, mean brook trout (*Salvelinus fontinalis*) density, elevation × mean brook trout density	8	−119.14	255.00	0.00	0.648
Elevation	6	−122.22	256.86	1.86	0.256
Elevation, mean brook trout density	7	−122.17	258.89	3.89	0.093
Elevation, mean width, wood density, mean brook trout density, elevation × mean brook trout density	17	−115.17	267.55	12.55	0.001
Elevation, mean width, wood density	15	−117.93	268.34	13.34	0.001
Mean temperature, mean width, wood density	15	−118.69	269.87	14.87	0.000
Elevation, mean width, wood density, mean brook trout density	16	−117.74	270.32	15.32	0.000
Mean temperature, mean width, wood density, mean brook trout density	16	−118.39	271.61	16.61	0.000
Mean temperature, mean width, wood density, mean brook trout density, mean temperature × mean brook trout density	17	−117.65	272.51	17.51	0.000
Mean temperature	6	−131.71	275.84	20.84	0.000
Mean temperature, mean brook trout density, mean temperature × mean brook trout density	8	−130.29	277.31	22.31	0.000
Mean temperature, mean brook trout density	7	−131.44	277.44	22.44	0.000
Mean temperature, elevation, mean width, wood density, mean brook trout density, mean temperature × mean brook trout density, elevation × mean brook trout density	24	−113.24	281.00	26.00	0.000
Mean width, wood density, mean brook trout density	11	−142.03	307.39	52.39	0.000
Mean brook trout density	4	−168.78	345.77	90.76	0.000

Note: Akaike weights are interpreted as relative plausibility of candidate models.

weights for two candidate models can be used to assess the degree of evidence for one model over another (Anderson et al. 2000), the confidence set of models included only those candidate models with Akaike weights that were within 10% of the largest weight (Thompson and Lee 2000), which is similar to the general rule of thumb (i.e., 1/8 or 12%) suggested by Royall (1997) for evaluating strength of evidence.

To allow for ease of interpretation of the relative magnitude of fixed and random effects, we plotted empirical Bayes (shrinkage) estimates (Snijders and Bosker 1999) of the relationship between site-level characteristics and bull trout density and presence for each stream using models within the confidence set. The precision of each fixed and random effect was estimated by computing 90% confidence intervals based on a t statistic with $n - 1$ degrees of freedom (Littell et al. 1996). The relative importance of individual predictor variables was estimated as the sum of Akaike weights for candidate models in which each predictor occurred (Burnham and Anderson 2002).

Results

In 1996, our lowest observations of bull trout ranged from about 1500 to 2000 m elevation (Fig. 2) in the streams we sampled. Mean temperatures ranged from 6.7 to 11.7 °C. The lowest observations and warmest temperatures associated with our observations of bull trout were in streams without brook trout. The streams with brook trout and bull trout tended to be narrower than the streams with bull trout alone.

In 1997, we observed bull trout more frequently in upper than in lower reaches sampled in each stream. When brook trout were present in a stream, we generally observed them in higher densities in the lower reaches we sampled (Fig. 3). Temperatures generally declined with elevation across streams, although the slope varied and in some cases temperature changed little or even increased slightly between a downstream and upstream thermograph.

Statistical analyses

Bull trout density

An examination of the normal probability plot of lower-level residuals from all candidate linear models relating site-specific characteristics and mean brook trout density to bull trout density indicated that the residuals departed from expected (i.e., the plots were curvilinear rather than linear). To normalize these data, we natural log transformed the data and refit the candidate models. An examination of normal probability plots of lower-level residuals and the χ^2 plots of the empirical Bayes residuals from each candidate model fit with the transformed data indicated that all of the models fit adequately.

The most plausible model of bull trout density contained elevation, mean brook trout density, and an elevation by mean brook trout density interaction and was 2.5 times more likely than the next best approximating model, which contained elevation alone (Table 4). The confidence set of models included these two and a third model that included elevation and mean brook trout density.

Elevation was positively related to small bull trout density across models (Table 5), but the relationship was highly variable among streams. The elevation random effect from the elevation-only model suggested that the influence of elevation (i.e., the parameter estimate) varied by more than 73% ($\sqrt{3.148}/2.420$) among streams (Table 5). The smaller

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Table 5. Estimates (standard error in parentheses) of fixed and random effects for confidence set of hierarchical linear models of bull trout (*Salvelinus confluentus*) density.

Parameter estimate	Estimate	90% confidence interval	
		Lower	Upper
Elevation, mean brook trout (*Salvelinus fontinalis*) density, elevation × mean brook trout density			
Fixed effect			
Intercept	−2.172 (0.847)	−3.561	−0.783
Elevation	1.510 (0.536)	0.631	2.388
Mean brook trout density	−10.472 (3.928)	−16.913	−4.031
Elevation × mean brook trout density	0.649 (0.246)	2.447	10.530
Random effect			
Intercept	4.228 (1.091)	2.439	6.016
Elevation	1.737 (0.691)	0.604	2.871
Residual	0.158		
Elevation			
Fixed effect			
Intercept	−3.653 (0.910)	−5.145	−2.161
Elevation	2.420 (0.565)	1.493	3.347
Random effect			
Intercept	8.046 (0.656)	6.971	9.122
Elevation	3.148 (0.417)	2.464	3.832
Residual	0.159		
Elevation, mean brook trout density			
Fixed effect			
Intercept	−3.614 (0.899)	−5.089	−2.139
Elevation	2.409 (0.561)	1.488	3.329
Mean brook trout density	−0.119 (0.275)	−0.571	0.332
Random effect			
Intercept	7.823 (1.905)	4.699	10.947
Elevation	3.098 (0.614)	2.091	4.106
Residual	0.159		

Note: Random effect estimate is a variance component.

elevation random effect in the model containing the elevation by mean brook trout density interaction (1.737) compared with the elevation random effect in the model without brook trout (3.148), suggested that 45% of this variation was attributed to mean brook trout density. Nonetheless, the remaining variation among streams was relatively high (Fig. 4*a*). The relationship between mean brook trout density and bull trout density was negative. The parameter estimate for mean brook trout density in the model without the elevation × brook trout interaction, however, was relatively small and imprecise, whereas the estimate was much larger and relatively precise for the model with the interaction.

Model predictions based on the model containing elevation, mean brook trout density, and their interaction (Table 5) indicated that bull trout density increased with elevation across a range of brook trout densities (Fig. 4*b*). At lower elevation sites (<1.5 km), our model predicted that bull trout were only present (i.e., density >0) when brook trout were absent in the stream. However, at higher elevation sites (>1.7 km), bull trout density was predicted to be greater in streams with relatively high brook trout densities.

Bull trout presence

The most plausible logit model of bull trout presence contained mean temperature, mean brook trout density, and a temperature by brook trout density interaction, but was only 1.06 times more likely than the next best approximating model that contained elevation only (Table 6). The confidence set of models included these two models and four others that contained either (*i*) temperature, mean brook trout density, and their interaction or (*ii*) elevation, mean brook trout density, and their interaction.

The confidence set of models indicated that bull trout presence was negatively and positively related to temperature and elevation, respectively. However, the temperature random effect in the temperature-only model suggested that the influence of temperature on bull trout presence varied as much as 54% among streams, whereas elevation varied as much as 40% among streams in the elevation-only model (Table 7). The smaller random effects in models containing the temperature by mean brook trout density and elevation by mean brook trout density interactions compared with models without interactions suggested that 24% and 51% of the variation in temperature and elevation effects, respectively, was attributed to mean brook trout density (Table 7). The remaining variation among streams, however, was relatively high when the brook trout density interaction was included in both the temperature and elevation models (Figs. 5*a* and 5*b*, respectively). Bull trout presence was positively and negatively related to brook trout density among

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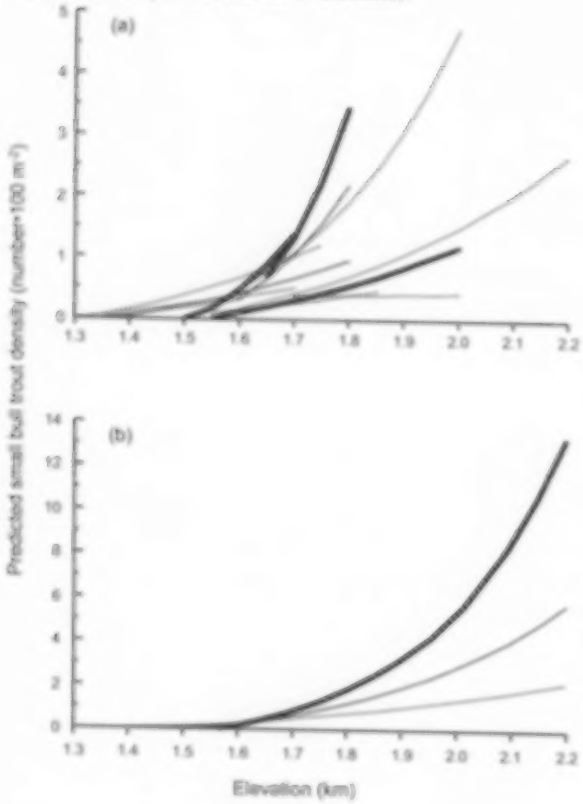
Fig. 4. Empirical Bayes estimates of the relationship between elevation and juvenile bull trout (*Salvelinus confluentus*) density for each of 12 study streams (*a*) and the average relationship between elevation and juvenile bull trout density for three levels of brook trout (*Salvelinus fontinalis*) density (*b*). Thin broken lines indicate no brook trout in the stream, and thin and heavy solid lines indicate streams with brook trout densities less than and greater than 0.4–100 m^{-2}, respectively. Stream-specific relationships in (*a*) are only plotted for the sampled range of elevations. The average relationship in (*b*) is based on the best-fitting hierarchical model of juvenile bull trout abundance.



models in the confidence set (Table 7), and parameter estimates were relatively imprecise (Table 7).

Model predictions based on the hierarchical logit model containing temperature, mean brook trout density, and their interaction indicated that the probability of bull trout presence increased with decreasing temperature across a range of brook trout densities (Fig. 6*a*). At temperatures >9 °C, the model suggested that the probability of bull trout presence was highest when brook trout were absent in the stream, but at colder temperatures (<9 °C) the probability of bull trout presence was highest in streams with high brook trout density (≥0.4–100 m^{-2}). In contrast, model predictions of bull trout presence based on the model containing elevation, mean brook trout density, and their interaction indicated the probability of presence increased with elevation across a range of brook trout densities (Fig. 6*b*). At relatively low elevations (<1600 m), the probability of presence was highest when brook trout were absent, whereas at high elevations the probability was highest when brook trout were abundant.

Contrasting models

For the linear models of bull trout density, the Akaike importance weights for elevation, mean brook trout density, and their interaction were more than 100 times greater than those of temperature, mean width, wood density, and the temperature by mean brook trout density interaction, which indicated that there was stronger evidence for the models with elevation (Table 8). In contrast, in the models of bull trout presence, importance weights for elevation and temperature were similar, indicating there was insufficient data to discern which was the more important predictor (Table 8). The brook trout effects were also more ambiguous in this group of models, suggesting the loss of information associated with the use of bull trout occurrence rather than density may be important.

Discussion

Samples of bull trout and brook trout exhibited the anticipated longitudinal patterns in density and occurrence. These patterns were generally consistent with other observations of complementary distributions of two or more ecologically similar salmonids occurring in mountain streams. Either temperature or elevation was the single most important variable explaining the distribution of bull trout. Brook trout were more abundant downstream of bull trout, and a brook trout effect was apparent in our models. Our results support the hypothesis that brook trout displace bull trout, although the results were highly variable, stream dependent, and uncertain at the scale of the entire population. Our results are also consistent with the hypothesis that a thermal gradient may influence both the patterns of occurrence of each species as well as their interactions.

A brook trout effect was included in the most plausible models in our analyses, although our results did not suggest the effect was dramatic or easily generalized. Brook trout density and interactions with elevation or estimated temperature were consistently important variables, but random effects (e.g., stream-level effects) were large, and predicted responses varied among streams. The coefficients associated with brook trout density also changed sign or varied in weight and precision among the most plausible models for either bull trout density or presence. The inclusion of the interaction terms helped clarify the response. Brook trout were associated with reduced density or probability of occurrence of bull trout at lower elevations or warmer temperatures, but also with higher bull trout density and probability of occurrence at higher elevations or colder temperatures. Higher probability of occurrence could be due to higher overall density because detection is a function of density and capture efficiency (Bayley and Peterson 2001). So on average, brook trout did appear to have displaced bull trout upstream, but they were not associated with a strong negative change in overall bull trout density or occurrence. Variable associations between bull trout and brook trout suggest that some (unknown) watershed-level factor(s) may influence overall fish production, while the distribution within a watershed is influenced by brook trout. The unknown factor(s) may be re-

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Table 6. Predictor variables, number of parameters (K), log-likelihood (Log$L$), Akaike's Information Criterion with the small-sample bias adjustment (AIC_c), ΔAIC_c, and Akaike weights (w) for the set of candidate models (i) for predicting bull trout (*Salvelinus confluentus*) presence.

Candidate model	K	Log$L$	AIC_c	ΔAIC_c	w_i
Mean temperature, mean brook trout (*Salvelinus fontinalis*) density, mean temperature × mean brook trout density	8	−280.99	578.70	0.00	0.284
Elevation	6	−283.20	578.82	0.12	0.267
Elevation, mean brook trout density, elevation × mean brook trout density	8	−281.70	580.11	1.41	0.140
Mean temperature	6	−283.89	580.19	1.49	0.135
Elevation, mean brook trout density	7	−283.19	580.94	2.24	0.092
Mean temperature, mean brook trout density	7	−283.31	581.18	2.48	0.082
Elevation, mean width, wood density, mean brook trout density, elevation × mean brook trout density	17	−279.17	595.54	16.83	0.000
Elevation, mean width, wood density	15	−281.78	596.04	17.34	0.000
Elevation, mean width, wood density, mean brook trout density	16	−281.19	597.22	18.52	0.000
Mean brook trout density	4	−296.83	601.86	23.16	0.000
Mean width, wood density, mean brook trout density	11	−291.17	605.68	26.98	0.000
Mean temperature, mean width, wood density, mean brook trout density, mean temperature × mean brook trout density	17	−284.35	605.91	27.21	0.000
Mean temperature, elevation, mean width, wood density, mean brook trout density, elevation × mean brook trout density, mean temperature × mean brook trout density	24	−277.17	608.87	30.17	0.000
Mean temperature, mean width, wood density	15	−289.50	611.48	32.78	0.000
Mean temperature, mean width, wood density, mean brook trout density	16	−297.27	629.37	50.67	0.000

Note: Akaike weights are interpreted as relative plausibility of candidate models.

lated to geology, soil productivity (e.g., Thompson and Lee 2000), or large-scale habitat features that were not included in our models.

The biological significance of displacement at the stream or local population level is not apparent in our data. We did not conduct complete population estimates, but the lack of an obvious change in densities suggests that brook trout have not had a dramatic influence on the absolute size of the bull trout populations in these streams. They may, however, constrain the area or size of the habitat that might be occupied by bull trout. Gunckel et al. (2002) demonstrated resource competition between brook trout and bull trout and concluded that brook trout are likely to displace bull trout when resources are scarce. They predicted that displaced bull trout would either be lost from the stream or be forced upstream into higher densities where intraspecific competition might reduce growth across the population. Our results suggest that the upstream displacement is likely, but they do not point to population-level effects.

Such an effect may still be important. Restriction of bull trout to a smaller area and a subsequent reduction in growth might reduce the resilience of a population and increase vulnerability to extirpation associated with environmental variation or catastrophic events. A reduction in available area might also reduce the extent and variability or complexity of habitats available to bull trout and thus restrict the number or extent of internal refugia available to populations experiencing extreme disturbances (e.g., fires and floods; Rieman and Clayton 1997; Dunham and Rieman 1999). Dunham and Rieman (1999) demonstrated a strong association between persistence of local bull trout populations and the size of local habitat patches. Habitat patches were defined as the watershed area above the point where temperatures become low enough to consistently support bull trout spawning and juvenile rearing. Morita and Yamamoto (2002) demonstrated a similar pattern for whitespotted char (*Salvelinus leucomaenis*) isolated in small streams by erosion control dams. In each case, local extinctions might be explained by a variety of genetic or demographic processes that follow from restriction in population size or from the demographic response suggested above. In either case, a population that is less resilient is more prone to either deterministic extinction or stochastic variation near the extinction threshold.

The magnitude of constraint in patch size implied by our data is not obvious, but some simple calculations provide perspective. Based on the most plausible models, it appears that the average displacement of the lower limit in bull trout distributions might be on the order of 100–200 m in elevation. The relative significance of that displacement will depend largely on the length of stream and channel gradients above that point. For example, in a stream with a mean gradient of 5% that initially had 10 km of habitat available for bull trout, an upstream displacement 200 m in elevation would represent a loss of 4 km (40%) of available stream; the loss would be greater in area if the stream becomes narrower upstream. In relative terms, the loss would be proportionally greater in smaller patches or with lower stream gradients and less in larger patches or with higher gradients. Such losses could equate to substantial increases in the extinction risk in patches that were already small, but might be insignificant for those that were large (Dunham and Rieman 1999).

Rich et al. (2003) provided evidence that brook trout and bull trout were more likely to coexist in larger streams, whereas brook trout may have eliminated bull trout in smaller streams. Brook trout also appear more likely to use small streams than large ones (Rich 1996), while bull trout appear less likely to persist in smaller streams (Rieman and

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Table 7. Estimates (standard error in parentheses) of fixed and random effects from best-fitting candidate hierarchical logistic regression models of bull trout (*Salvelinus confluentus*) presence.

Parameter estimate	Estimate	90% confidence interval	
		Lower	Upper
Mean temperature, mean brook trout (*Salvelinus fontinalis*) density, mean temperature × mean brook trout density			
Fixed effect			
Intercept	10.506 (3.775)	4.315	16.696
Mean temperature	−1.043 (0.364)	−1.640	−0.446
Mean brook trout density	28.946 (17.077)	0.940	56.952
Mean temperature × mean brook trout density	−3.109 (1.767)	−6.006	−0.211
Random effect			
Intercept	53.354 (8.623)	39.212	67.496
Mean temperature	0.466 (0.075)	0.343	0.590
Elevation			
Fixed effect			
Intercept	−21.313 (3.937)	−27.770	−14.856
Elevation	12.455 (2.380)	8.552	16.358
Random effect			
Intercept	63.295 (31.807)	11.132	115.458
Elevation	24.897 (11.473)	6.081	43.714
Elevation, mean brook trout density, elevation × mean brook trout density			
Fixed effect			
Intercept	−16.136 (3.907)	−22.544	−9.727
Elevation	9.369 (2.446)	5.357	13.380
Mean brook trout density	−45.039 (21.867)	−80.901	−9.178
Elevation × mean brook trout density	26.754 (13.317)	4.915	48.594
Random effect			
Intercept	21.967 (14.330)	0.000	45.469
Elevation	12.165 (8.450)	0.000	26.023
Mean temperature			
Fixed effect			
Intercept	14.162 (3.262)	8.812	19.511
Mean temperature	−1.440 (0.326)	−1.975	−0.904
Random effect			
Intercept	61.316 (12.828)	40.279	82.353
Mean temperature	0.610 (0.165)	0.339	0.881
Elevation, mean brook trout density			
Fixed effect			
Intercept	−21.475 (3.988)	−28.015	−14.936
Elevation	12.658 (2.429)	8.675	16.642
Mean brook trout density	−1.051 (2.030)	−4.380	2.279
Random effect			
Intercept	64.350 (29.58)	15.842	112.857
Elevation	26.224 (8.32)	12.586	39.861
Mean temperature, mean brook trout density			
Fixed effect			
Intercept	14.624 (3.442)	8.979	20.269
Mean temperature	−1.452 (0.337)	−2.004	−0.900
Mean brook trout density	−1.985 (1.923)	−5.138	1.168
Random effect			
Intercept	70.910 (13.72)	48.416	93.404
Mean temperature	0.670 (0.14)	0.445	0.895

Note: Random effect estimate is a variance component.

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Table 8. Akaike importance weights for parameters from candidate models of bull trout (*Salvelinus confluentus*) density and presence.

Model parameter[a]	No. of candidate models	Importance weights	
		Small[b] bull trout density	Bull trout presence
Elevation	7	0.999	0.500
Mean temperature	7	0.001	0.500
Mean width	8	0.003	0.000
Wood density	8	0.003	0.000
Mean brook trout (*Salvelinus fontinalis*) density	11	0.743	0.598
Elevation × mean brook trout density	3	0.649	0.140
Mean temperature × mean brook trout density	3	0.000	0.284

Note: Importance weights were estimated as the sum of Akaike weights from individual candidate models containing the parameter.

[a]The intercept was included in all candidate models; hence, the importance weight equals one.

[b]<150 mm.

Fig. 5. Empirical Bayes estimates of the relationship between temperature (*a*) and elevation (*b*) and the probability of bull trout (*Salvelinus confluentus*) presence for each of 12 study streams. Thin broken lines indicate no brook trout (*Salvelinus fontinalis*) in the stream, and thin and heavy solid lines indicate streams with brook trout densities less than and greater than 0.4–100 m^{-2}, respectively. Stream-specific lines are only plotted for the sampled range of temperatures.

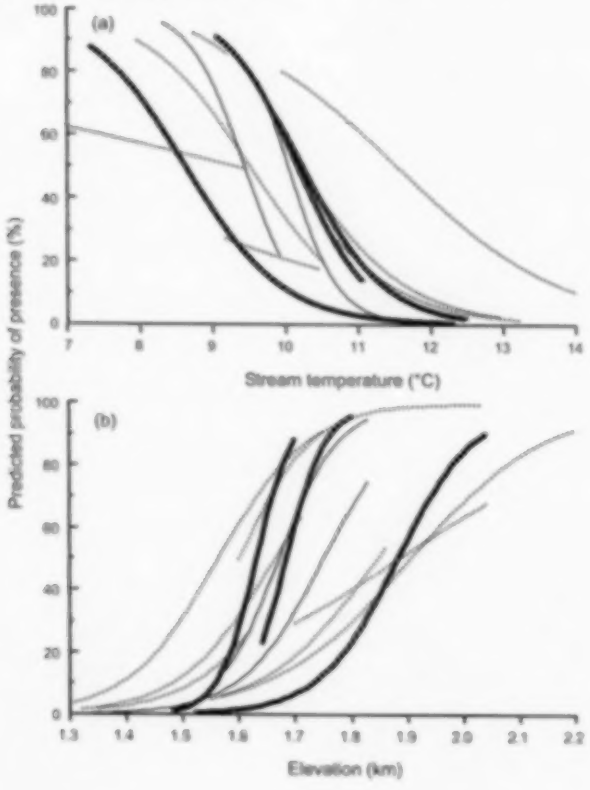
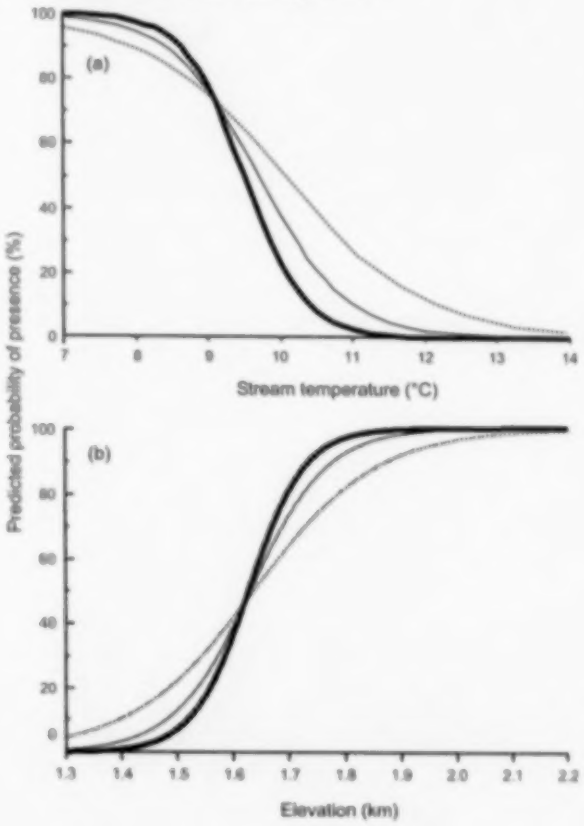


Fig. 6. The average relationship between temperature (*a*) and elevation (*b*) and the probability of bull trout (*Salvelinus confluentus*) presence for three levels of mean brook trout (*Salvelinus fontinalis*) density. Thin broken lines indicate no brook trout in the stream, and thin and heavy solid lines indicate streams with brook trout densities less than and greater than 0.4–100 m^{-2}, respectively. Predictions were based on best-fitting hierarchical models of bull trout presence.



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McIntyre 1995; Dunham and Rieman 1999). It may be that brook trout hold some ecological advantage in small streams. Because small streams are associated with small patches (Rieman and McIntyre 1995), it might also be that any interaction and upstream displacement of bull trout by brook trout ultimately holds greater consequences in terms of patch-level extinction processes in small streams than in large ones.

Our results add to evidence that introduced brook trout can displace native salmonids, including bull trout. Invasion could influence the persistence of populations even if displacement is incomplete, but the population-level consequences of these effects remain an important question. In some systems, local extinctions of native species have followed the establishment of brook trout (M. Enk, US Forest Service, 1101 15th Street North, Great Falls, MT 59405, USA, personal communication), while the species coexist in others. In our streams, we found evidence that brook trout have had an effect, but these bull trout populations have obviously persisted with modest numbers of individuals. Because we nonrandomly selected study streams where we knew bull trout occurred, our observations may not represent the future for all populations threatened by brook trout invasion. It may be that the displacement predicted from our models is a measure of a "debt of extinction" yet to be paid (Hanski 1996) or of the resistance of bull trout on the brook trout invasion front.

Brook trout probably do displace bull trout and may well catalyze if not directly cause local extinctions. Obviously, from a native species-conservation perspective, further introductions of brook trout or management that favors their expansion into the range of native species (e.g., the stocking or maintenance of populations in headwater lakes; Adams et al. 2001) is imprudent. Despite the obvious threats, however, our work and other studies (see Dunham et al. 2002*a* for a review) indicate the influence of brook trout at both a habitat scale and stream or population scales is highly variable. The complete elimination of bull trout or other species is not a foregone conclusion. Brook trout have not invaded all of the habitats accessible to them (Adams et al. 2002) or eliminated native species in many places where they co-occur (Dunham and Rieman 1999; Rich et al. 2003). Longer-term studies also indicate that some populations of native salmonids can persist in the face of invasions and habitat loss (Strange and Habera 1998; Meyer et al. 2003).

Continued efforts to understand the population and landscape-level patterns of brook trout invasion, species displacement, and subsequent local extinctions could prove critical to management that must prioritize limited conservation resources or controversial control measures. Manipulative experiments will be important to understand the underlying mechanisms in any detail. However, broadly replicated studies and newer statistical methods examining the patterns of distribution within streams distributed over large regions could add substantially to knowledge of where threats exist. Our results suggest that even simple occurrence data (as opposed to density) can be useful for detecting important patterns; although some information is lost, the potential to sample extensively could help clarify this issue.

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Experimental determination of the sources of otolith carbon and associated isotopic fractionation

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Abstract: Otolith stable carbon isotope ratios provide a unique and widely applicable environmental record. Unfortunately, uncertainty regarding the proportion of otolith carbon that derives from metabolized food versus dissolved inorganic carbon (DIC) in the water currently limits utilization of this marker. We manipulated the $\delta^{13}C$ of food and ambient DIC in a factorial design with juvenile rainbow trout (*Oncorhynchus mykiss*). At the activity levels and total metabolic rates characteristic of fish in this study, 17% (±3% standard error, SE) of otolith C was metabolically derived, while >80% was derived from DIC in ambient water. We also estimated isotopic enrichment factors associated with physiological carbon transformations by measuring $\delta^{13}C$ of blood and endolymph (which closely tracked otolith $\delta^{13}C$). There was substantial depletion in ^{13}C of blood relative to C sources ($\varepsilon_{blood-source}$ = –16.9‰ ± 1.1‰ SE), but substantial enrichment in ^{13}C in otolith relative to blood ($\varepsilon_{oto-blood}$ =13.3‰ ± 1.3‰ SE). Net isotopic enrichment between sources and the otolith was therefore slightly negative. Most of the isotopic enrichment between the blood and the otolith was associated with the movement of C from blood to endolymph, while enrichment associated with the precipitation of otolith aragonite from the endolymph was small.

Résumé : Les rapports des isotopes stables de carbone dans les otolithes représentent une rétrospective des conditions du milieu qui est à la fois exceptionnelle et d'utilisation multiple. Malheureusement, des incertitudes concernant la proportion du carbone dans les otolithes qui provient de la nourriture métabolisée par rapport au carbone inorganique dissous (DIC) dans l'eau freinent actuellement l'utilisation de ce marqueur. Nous avons fait varier le $\delta^{13}C$ de la nourriture et du DIC ambiant selon un plan d'expérience factoriel avec de jeunes truites arc-en-ciel (*Oncorhynchus mykiss*). Aux niveaux d'activité et aux taux métaboliques caractéristiques des poissons utilisés dans notre étude, 17 % (±3 % erreur type, ET) du C des otolithes provient du métabolisme, alors que >80 % vient du DIC de l'eau ambiante. Nous avons aussi mesuré les facteurs d'enrichissement métabolique associés aux transformations physiologiques du carbone, en déterminant le $\delta^{13}C$ du sang et de l'endolymphe (qui suit de près le $\delta^{13}C$ des otolithes). Il y a une perte substantielle de ^{13}C dans le sang par rapport aux sources de C ($\varepsilon_{sang-sources}$ = –16,9‰ ± 1,1‰ ET), mais aussi un enrichissement important de ^{13}C dans les otolithes par rapport au sang ($\varepsilon_{oto-sang}$ = 13,3‰ ± 1,3‰ ET). L'enrichissement isotopique net des sources vers les otolithes est donc légèrement négatif. La majorité de l'enrichissement isotopique entre le sang et les otolithes est associée au passage du C du sang vers l'endolymphe, alors que l'enrichissement dû à la précipitation d'aragonite dans les otolithes depuis l'endolymphe est faible.

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Introduction

All teleost fishes possess bilaterally symmetric sets of three otoliths (the sagittae, lapilli, and asterisci), which are involved in sensory perception and are contained within the vestibular apparati of the inner ear. Approximately 95% of the mass of otoliths is composed of calcium carbonate, which precipitates onto a protein matrix from the bicarbonate-rich endolymph fluid that fills the vestibular apparatus (Campana and Neilson 1985; Payan et al. 1997; Tohse and Mugiya 2002). Precipitation occurs in distinct bands, often with daily periodicity (Pannella 1971), and the precipitated material reflects the chemical and isotopic composition of the fish's prey and ambient water (Campana 1999). Furthermore, unlike other calcified tissues, otoliths remain metabolically inert throughout the life of the fish (Campana and Neilson 1985). Therefore, otoliths preserve a continuous and finely resolved record of the fish's environment.

Otolith stable carbon (C) isotope ratios potentially represent an informative and versatile part of this environmental record. Because C isotope ratios in food webs vary considerably as a result of physiological isotopic fractionations by primary producers and decomposers, aquatic and terrestrial ecologists commonly use them to study trophic structure and migration (Peterson and Fry 1987; Hobson 1999). Studies of otoliths from marine and freshwater fishes have used stable isotope ratios of C (sometimes in conjunction with oxygen) to identify stocks for fisheries management (Edmonds and Fletcher 1997; Stephenson et al. 2001; Bastow et al. 2002), elucidate natal origin and migration patterns across very small (Dufour et al. 1998) or relatively large (Nelson et al. 1989; Northcote et al. 1992; Gao and Beamish 1999) spatial extents, infer environmental or autecological change (Schwarcz et al. 1998; Weidman and Millner 2000; Begg and Weidman 2001), and study metabolic history (Kalish 1991*a*; Schwarcz et al. 1998). Patterns of migration and metabolic rate ontogeny have also been determined for ancient fishes using C isotopes in fossilized otoliths (Carpenter et al. 2003; Wurster and Patterson 2003).

Unfortunately, uncertainty regarding the sources of otolith C and the magnitude of physiological isotope fractionations associated with otolith precipitation currently limits the utility of this marker. Indeed, of the 13 recent studies of otolith C isotopes cited above, 5 (40%) qualified their results with a statement regarding this uncertainty. Without a first-principles basis for understanding temporal and individual variation in otolith C isotopes, most studies have relied on descriptive or correlative analysis of observed patterns. Such methods, while valid and useful, are clearly limiting. For instance, Weidman and Millner (2000) observed consistent trends in otolith C isotope ratios of North Atlantic cod, but noted that their ability to distinguish among dietary, physiological, and temperature-related explanations for these trends was limited by poor knowledge of conditions and feeding in the wild. The converse is also true and probably more important for those who would apply these techniques to practical problems; without knowing what determines otolith C isotopes, we cannot fully capitalize on the information that they may provide about environmental conditions and fish behavior.

Possible sources of C to the otolith include C in the fish's prey and dissolved inorganic carbon (DIC) in the environment (i.e., ambient water). Metabolized C from the prey enters the bloodstream and thence, presumably, the endolymph fluid; otolith C that follows this path is referred to as metabolic carbon. The pathway from water DIC to otolith C is less clear. To understand otolith C isotope ratios, it is necessary to determine the relative contribution of these two sources, as well as the magnitude of any isotopic fractionation that occurs along the physiological pathway from source to otolith. Early studies confirmed that some proportion of otolith C is metabolically derived (Radtke 1984; Kalish 1991*a*; Thorrold et al. 1997). Recent experimental (Kalish 1991*b*; Høie et al. 2003; Tohse and Mugiya 2004) and observational (Schwarcz et al. 1998; Weidman and Millner 2000) estimates of the proportion of metabolic C (denoted M) are generally between 0.10 and 0.40, although Wurster and Patterson (2003) suggested that M may change by as much as 0.95 during the course of a fish's life (corresponding to variation in M from as much as 0.95–1.00 to as little as 0–0.05). Yet only one of these studies controlled for variation in the C isotopic composition of both food and water (Tohse and Mugiya 2004), and few have considered potential physical or physiological fractionation of isotopes.

In this study, we raised juvenile rainbow trout (*Oncorhynchus mykiss*) at two different levels of water DIC $\delta^{13}C$ on one of three nutritionally identical but isotopically distinct feeds. We estimated fractionation factors associated with otolith precipitation by measuring $\delta^{13}C$ of the otolith, blood DIC, and endolymph DIC.

Methods

Experimental design

To determine the relative contributions of water DIC and food C to otolith C, we raised rainbow trout and manipulated the $\delta^{13}C$ of these two C sources in a 2 × 3 factorial design. We applied the treatments to five complete randomized blocks of six flow-through aquaria filled with 25 L of water from a groundwater source (alkalinity ~360 mg·L^{-1}, pH ~8.2). Each block was contained in a large flow-through trough of cold surface water to reduce water temperature in the aquaria; the mean (± standard deviation; n=4783) water temperature experienced by fish during the experiment ranged from 14.4 ± 0.5 °C to 15.2 ± 0.7 °C in 12 continuously monitored aquaria. We adjusted the rate of flow into each aquarium every 3–4 days to 200 ± 5 mL·min^{-1}.

Thirty trout obtained from a California state fish hatchery were randomly assigned to individual aquaria. Initial fork length of these fish was 128 ± 10 mm (mean ± standard error (SE)). Two days before the start of the experiment, we added 2.25 g of the bone stain Alizarin Red S to each aquarium, turned off the incoming water, held fish in a 90 mg·L^{-1} bath of Alizarin Red S for 6 h, and then slowly flushed the bath with fresh water. We applied this treatment because Alizarin Red S is incorporated into otoliths and can be seen under epifluorescent illumination as a bright red band (Beckman and Schulz 1996; Lagardère et al. 2000), allowing us to distinguish without ambiguity the beginning of the experimental period in subsequent examination and sampling of otoliths. All use of fish in this experiment was in accordance with Institutional Animal Care and Use Committee (IACUC) protocol #10407.

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We fed fish one of three nutritionally identical feeds that differed only in their C isotope ratio. Three batches of house fly larvae (*Musca domestica*) were raised on a manure substrate (Oregon Feeder Insects, Tillamook, Oregon). In two batches, we altered the C isotope ratio of the growth substrate by mixing in 2 or 4 g of ^{13}C-enriched algal cells (^{13}C lyophilized algal cells, 99 atom %; Isotec, Inc., Miamisburg, Ohio). When *M. domestica* neared the end of the larval stage, they were removed from the growth substrate, given 24 h to clear their guts, and then flash-frozen. Larvae remained frozen until ~10 min before being fed to fish. We refer to flies from the unlabeled, 2 g labeled, and 4 g labeled batches as the low, medium, and high δ^{13}C food treatments, respectively. Analyses of *M. domestica* larvae indicate that they provide nutritional value very similar to that of formulated trout feeds (S. Cockerum, Oregon Feeder Insects, P.O. Box 714, Tillamook, OR 97141-0714, USA, unpublished data).

To reduce the potential for food C to leach into the water in the aquaria (thereby confounding the water δ^{13}C manipulation), we took two precautions. First, we fed fish at a ration slightly below satiation, thus ensuring that no uneaten larvae remained in the aquaria after feeding. This ration (fed twice daily, at 0900 and 1600) increased from 0.2 to 0.4 g of *M. domestica* larvae per fish over the course of the 20-day experiment. Second, after each afternoon feeding, we siphoned tanks clean of feces.

We manipulated the C isotope ratio of the water in the aquaria by adding ^{13}C-enriched sodium bicarbonate ($NaH^{13}CO_3$, 98 atom %; Isotec, Inc., Miamisburg, Ohio). The polyvinyl chloride trunk line supplying well water to the experimental system was split "upstream" of the first block of aquaria; each of the two resulting branches fed half of the aquaria in each block. We did not alter the δ^{13}C of the DIC in one branch; this branch supplied water to all of the aquaria randomly assigned to the "well" water treatment. Just downstream of the branch point, we used a peristaltic pump to deliver 4 mL·min^{-1} of a bicarbonate spike into the second branch, which supplied water to all of the aquaria randomly assigned to the "spike" water treatment. We mixed 9.87 g of $NaH^{13}CO_3$ into 20 L of well water to make the bicarbonate spike, which was stored in a large media bag (resistant to CO_2 and water vapor diffusion; Nalge Nunc International, Rochester, New York). We mixed a new 20 L batch of spike every 3–4 days.

Sampling

At the beginning of the experiment, we randomly selected 15 *M. domestica* larvae from each of the three food treatments and dried them at 60 °C for 1–2 days in preparation for determination of stable C isotope ratios (described below).

To produce a temporally integrated estimate of DIC δ^{13}C for each aquarium, we took water samples on 11 separate occasions spanning the course of the experiment. We chose sampling days and times to check for both diel and long-term variation in DIC δ^{13}C. We overfilled a threaded, 20 mL glass EPA vial by submerging it in the aquarium, then poisoned it with ~50 µL of saturated mercuric chloride, and closed it tightly with a screw-on polypropylene cap lined with a 32 mm (0.125 inch) tetrafluoroethylene–silicone septum. Total time of exposure to the atmosphere was <1 min for each sample. Sampling precision for δ^{13}C DIC measurements was 0.6 ‰ for well water samples (average standard error of n = 6 pairs of duplicate samples) and 3.8 ‰ for spiked water samples (n = 7 duplicate pairs). Preserved samples were kept refrigerated and in the dark until analysis, when we drew a 10 µL aliquot and injected it into 1 mL of 85% phosphoric acid in a sealed autosampler vial that had been evacuated of atmospheric air and filled with nitrogen gas.

Fish were fed for the last time on the afternoon of day 19. We sampled fish blood and endolymph, extracted otoliths, and took muscle tissue samples beginning at 1130 on day 20. We anesthetized each fish by adding an overdose of tricaine methanesulfonate (500 mg·L^{-1}, buffered to aquarium pH of 8.2) to its aquarium. Once the fish was unconscious, but while it was still visibly breathing, we sampled <100 µL of blood via cardiac puncture using gas-tight syringes and needles (Houston 1990). We immediately injected ~10 µL of blood into phosphoric acid in a sealed autosampler vial, as described above. Acidifying blood in this way should drive off, as CO_2(g), all DIC present either in solution or bound to red blood cells. Sampling precision for blood δ^{13}C measurements was 1.8 ‰ (average SE of n = 5 duplicate pairs).

After sampling blood, we killed the fish by spinal transection near the posterior margin of the operculum, allowed blood to drain from the head for ~1 min, and exposed and removed the brain tissue. After severing the semicircular canals that connect the various sacs of the left vestibular apparatus, we gently removed the entire apparatus and placed it under a dissecting microscope. Using a gas-tight syringe with a 26-gauge, small-bore needle, we drew a small sample (usually ~0.5 µL; range 0.3–3.0 µL) of endolymph fluid from one of the vestibules of the apparatus (usually the saccular vestibule, which contains the sagitta). This endolymph was immediately injected into phosphoric acid in an autosampler vial, as described above. We then extracted the sagitta from the saccular vestibule and removed any adherent bits of tissue; all extracted sagittae were held at room temperature for 2–8 h and then placed in a drying oven at 60 °C for 72 h. After completing the extraction of the left sagitta, we repeated the entire procedure with the right vestibular apparatus and sagitta. This entire procedure took ~20–30 minutes per fish. Because the volume of endolymph fluid present was sufficient for only one sample per fish, we injected endolymph from the right saccular vestibule into the same vial as endolymph from the left. Even so, the combined volume was often not sufficient for accurate determination of δ^{13}C. We carefully screened the results of endolymph isotopic ratio analyses (described below) and discarded data when samples did not produce a sufficiently large peak for accurate determination of δ^{13}C.

Otoliths were mounted on glass slides and sectioned to reveal banding patterns (Secor et al. 1991). Otolith material was sampled using a computer-controlled micromill (width of milling bit at tip = 50 µm) linked to a scope camera (New Wave Research, Fremont, California). This enabled us to sample as little as 20 µm of the most recent growth at the otolith edge. Before milling, we photographed polished otoliths using epifluorescent microscopy (450–490 nm excitation filter, 510 nm dichroic filter, and 520 nm long pass

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emission filter) and mapped areas where the band marked with Alizarin Red S was sufficiently far from the edge of the otolith to minimize the risk of sampling pre-experiment otolith material. The total mass of otolith material sampled for each otolith was usually about 10–15 μg.

Determination of stable isotope ratios

We determined the C isotope ratios of all liquid samples (water, blood, and endolymph) using a PerkinElmer headspace sampler (PerkinElmer, Wellesley, Massachusetts) attached to a Micromass (VG Instruments, Manchester, UK) IsoPrime isotope ratio mass spectrometer (IRMS) at the Center for Isotope Geochemistry of Lawrence Berkeley National Laboratory (Berkeley, California). Autosampler vials with blood or endolymph samples were refrigerated for 1–2 days until analysis. Otolith aragonite samples were analyzed at the Department of Geology, University of California – Davis. Samples were pretreated by heating in vacuo at 75 °C for 30 min and then converted to CO_2 in a heated (90 °C) acid bath. Purified gas was introduced into a Micromass Optima IRMS, which measured $\delta^{13}C$ (V-PDB) by comparison with a standard reference gas calibrated to NBS-19. Average precision of the instrument for $\delta^{13}C$ is ± 0.04 ‰ (1 σ).

Calculations and statistical analyses

Sources of C to the otolith include the fish's prey and the DIC in ambient water. Along the pathway from source to otolith, physicochemical and biological processes may alter the stable isotope ratio of C from these sources. The C isotopic composition of the otolith can therefore be described by a two end-member mixing model that incorporates isotopic enrichment:

$$(1)\quad \delta^{13}C_{oto} = M(\delta^{13}C_{food} + \varepsilon_{blood-food}) + (1 - M)(\delta^{13}C_{water} + \varepsilon_{blood-water}) + \varepsilon_{endo-blood} + \varepsilon_{oto-endo}$$

where $\delta^{13}C_{oto}$, $\delta^{13}C_{food}$, and $\delta^{13}C_{water}$ represent the stable C isotopic composition of, respectively, the otolith, the food that the fish eats, and the DIC in ambient water; M is the proportion of metabolically derived C in the otolith; $\varepsilon_{blood-food}$ and $\varepsilon_{blood-water}$ are isotopic enrichment factors describing how isotopes are fractionated as C makes its way from ingested food or ambient water, respectively, to the blood; $\varepsilon_{endo-blood}$ is the isotopic enrichment as C moves from the blood into the endolymph; and $\varepsilon_{oto-endo}$ represents the isotopic enrichment as otolith aragonite precipitates from DIC in the endolymph. These enrichment factors are calculated as follows:

$$(2)\quad \varepsilon_{A-B} = (\alpha - 1)(1000)$$

where α is the isotopic fractionation factor relating the stable isotope ratio of substance A to that of substance B:

$$(3)\quad \alpha = R_A / R_B$$

We were unable to uniquely estimate $\varepsilon_{blood-food}$ and $\varepsilon_{blood-water}$ because our experimental design cannot distinguish between (*i*) mixing of food and water C sources in the blood and (*ii*) isotopic enrichment of C from these sources as it enters the blood. Note that by rearranging eq. 1, it is possible to express all of the enrichment terms as one ε_{total}:

$$(4)\quad \varepsilon_{total} = M(\varepsilon_{blood-food} - \varepsilon_{blood-water}) + \varepsilon_{blood-water} + \varepsilon_{endo-blood} + \varepsilon_{oto-endo}$$

which represents the net effect of all of the isotopic fractionations that may occur between C sources and the otolith. We therefore solved for M by multiple linear regression using the following equation:

$$(5)\quad \delta^{13}C_{oto} = \beta_1 \delta^{13}C_{food} + \beta_2 \delta^{13}C_{water} + \beta_0$$

where β_0 represents ε_{total} and M is given by the proportion of the total effect of food and water on otolith $\delta^{13}C$ that is attributable to food:

$$(6)\quad M = \beta_1 / (\beta_1 + \beta_2)$$

Because the proportion of metabolic C in the otolith should be the same as that in the blood, we also calculated M according to eq. 6 using a version of eq. 5 that has $\delta^{13}C_{blood}$ as the dependent variable. Uncertainty in M was estimated using first-order, second-moment error propagation:

$$(7)\quad \sigma_{f(x_j)} \approx \sqrt{\sum_{j=1}^{m} \left\{ \frac{\partial [f(x_j)]}{\partial x_j} \sigma_{x_j} \right\}^2 + 2 \sum_{j=1}^{m} \sum_{k=j+1}^{m} r_{x_j x_k} \left\{ \frac{\partial [f(x_j)]}{\partial x_j} \sigma_{x_j} \right\} \left\{ \frac{\partial [f(x_j)]}{\partial x_k} \sigma_{x_k} \right\}}$$

where $f(x_j)$ is the function used to estimate the parameter, m is the number of variables, x_j, and $r_{x_j x_k}$ is the correlation between parameters.

Using eq. 2 and measured $\delta^{13}C$ of food, water, blood, endolymph, and otolith, we calculated empirical estimates of several components of ε_{total}. We calculated mean $\varepsilon_{endo-blood}$ and $\varepsilon_{oto-endo}$ across all fish using measured $\delta^{13}C_{blood}$, $\delta^{13}C_{endo}$, and $\delta^{13}C_{oto}$. The isotopic enrichment from C sources to the blood ($\varepsilon_{blood-sources} = M(\varepsilon_{blood-food} - \varepsilon_{blood-water}) + \varepsilon_{blood-water}$) was calculated based on $\delta^{13}C_{blood}$ and the expected $\delta^{13}C$ of the blood if it were a combination ($M\delta^{13}C_{food} + (1 - M)\delta^{13}C_{water}$) of end members with no fractionation. Enrichment from blood to the otolith ($\varepsilon_{oto-blood} = \varepsilon_{endo-blood} + \varepsilon_{oto-endo}$) was calculated from $\delta^{13}C_{blood}$ and

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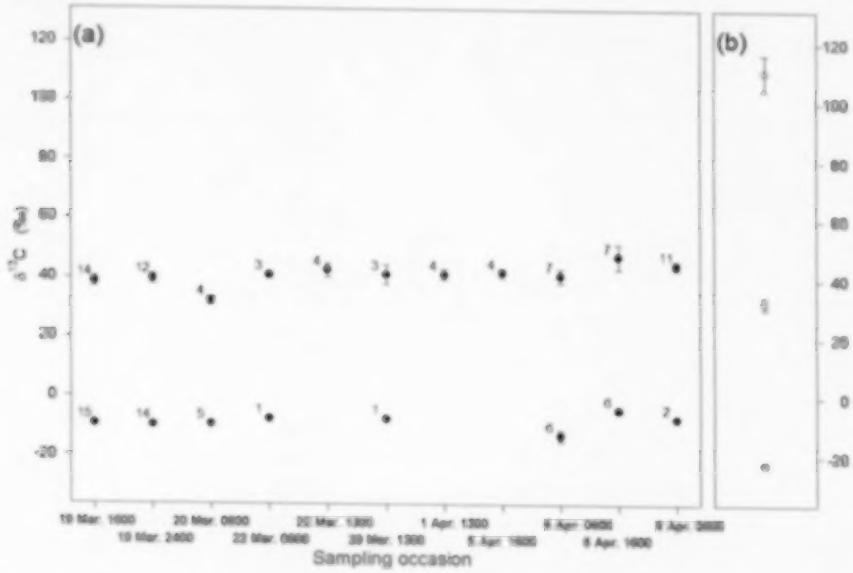
Fig. 1. Stable carbon (C) isotope ratios of potential sources of otolith C in this experiment. (*a*) $\delta^{13}C$ of water dissolved inorganic carbon (DIC). Date and time of each sampling occasion are given on the *x* axis. Each solid circle represents the mean (±1 standard error, SE) $\delta^{13}C$ DIC of all aquaria measured on that day in either the well (unaltered well water) or spike (well water spiked with $NaH^{13}CO_3$) treatments. Sample size is given next to each point. (*b*) Open circles give mean (±1 SE, $n = 15$) $\delta^{13}C$ of *Musca domestica* larvae used to feed fish in the three food treatments.



$\delta^{13}C_{water}$. All analyses were performed in the R statistical package (Version 1.9.1; R Development Core Team 2004).

Results

Our manipulations of end member $\delta^{13}C$ produced large and consistent differences. Constant addition of a ^{13}C bicarbonate spike to well water successfully differentiated $\delta^{13}C$ DIC isotopic composition of the spiked and well water treatments (Fig. 1; Table 1). On 11 sampling occasions spanning the course of the experiment, $\delta^{13}C$ DIC averaged –9.1‰ ± 0.4‰ (mean±SE, $n = 50$) in the well water treatment and 41.2 ‰ ± 0.8‰ ($n = 73$) in the spike treatment. We also created large differences in $\delta^{13}C$ of three nutritionally identical fish feeds by culturing *M. domestica* larvae on substrates spiked with varying amounts of ^{13}C algal cells (Fig. 1; Table 1).

All fish grew and remained healthy throughout the experiment. However, upon dissection we observed that many had partially or completely vateritic sagittal otoliths, as opposed to fully aragonitic otoliths (16 of 60 otoliths were at least partially vateritic). Vaterite is an alternate crystal form of calcium carbonate that sometimes occurs in otoliths, but which masks the usual banding patterns. Consequently, we were unable to accurately sample otolith material from the experimental period in these cases and excluded these otoliths from the analysis. In addition, stable isotope analysis of otolith material occasionally failed because of insufficient mass, since our sample size (as low as 10 µg in some cases) was at the limit of the capabilities of the mass spectrometer. For two individuals, analysis failed for both otoliths. Finally, one additional fish was excluded from the data set because a considerable amount of the epoxy used to mount the otoliths was accidentally included with the microsample of otolith material. In total, data from 25 out of 30 fish were used in our model.

Otolith $\delta^{13}C$ increased with both $\delta^{13}C_{water}$ and $\delta^{13}C_{food}$, although $\delta^{13}C_{water}$ was clearly the primary driver of otolith $\delta^{13}C$ (Fig. 2). The response of blood and endolymph stable C isotope ratios to the experimental manipulations was similar to that of otoliths (Fig. 3). We estimated the proportion of metabolic C in the otolith (eqs. 5 and 6) and the standard error of this estimate (eq. 7) as $M = 0.15 \pm 0.04$ (model $R^2 = 0.87$). Similarly, the model fit with $\delta^{13}C_{blood}$ as the response estimated $M = 0.17 \pm 0.03$ (model $R^2 = 0.91$). Sampling by micromill apparently did incorporate some pre-experiment otolith material in at least some cases; in the spike–medium and spike–high treatments, where the large $\delta^{13}C$ difference between otolith laid down before versus during the experiment enabled detection of such contamination, four otoliths had $\delta^{13}C$ substantially below either of the end members (Fig. 2). Analysis of two otoliths by ion microprobe confirmed this interpretation, yielding a value similar to our IRMS value for an otolith from the well–low treatment but a higher value than our IRMS value for an otolith from the spike–high treatment (P. Weber, unpublished data). Any contamination of spike–medium and spike–high otolith samples with pre-experiment otolith material had little effect on the results; using a reduced model that excludes all of the otoliths in these treatments changed the estimate of M only to 0.17 ± 0.03 (and R^2 to 0.90). Because the reduced otolith model and the blood model produced identical results, we chose $M = 0.17$ as the best point estimate for the proportion of metabolic C in the otolith.

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Table 1. Carbon (C) isotope composition of fish tissues (blood, endolymph, and otolith) and end members (food and dissolved inorganic carbon (DIC) in water).

		$\delta^{13}C$								
Fish ID	Treatment	Water DIC	Food	Blood	Endolymph	Otolith	ε_{total}	$\varepsilon_{oto-blood}$	$\varepsilon_{endo-blood}$	$\varepsilon_{oto-endo}$
1	Well–low	–10.9	–22.51	–29.1	—	—	—	—	—	—
2	Well–medium	–9.5	32.14	–12.7	–4.8	–4.40	–3.2	8.4	8.1	0.4
3	Well–high	–8.8	110.15	–9.0	8.5	11.77	–3.0	21.0	17.7	3.2
4	Spike–low	38.9	–22.51	15.1	23.0	18.75	–7.8	3.6	7.7	–4.1
5	Spike–medium	39.7	32.14	27.4	35.8	14.14	–23.2	–12.9	8.2	–20.9
6	Spike–high	40.1	110.15	31.7	—	—	—	—	—	—
7	Well–low	–9.3	–22.15	–28.2	—	–11.10	0.8	17.6	—	—
8	Well–medium	–7.3	32.14	–24.4	–3.0	–4.82	–5.3	20.0	21.9	–1.8
9	Well–high	–7.9	110.15	–12.3	—	6.95	–8.4	19.5	—	—
10	Spike–low	37.1	–22.51	10.5	23.4	29.37	4.0	18.7	12.7	5.9
11	Spike–medium	37.3	32.14	27.2	—	—	—	—	—	—
12	Spike–high	39.3	110.15	16.6	—	41.24	–11.5	24.2	—	—
13	Well–low	–10.4	–22.51	–25.2	—	–12.62	0.2	12.9	—	—
14	Well–medium	–9.3	32.14	–18.2	–7.6	–7.96	–6.9	10.5	10.8	–0.3
15	Well–high	–11.7	110.15	–0.5	—	7.53	–4.9	8.0	—	—
16	Spike–low	41.6	–22.51	20.6	—	—	—	—	—	—
17	Spike–medium	44.7	32.14	28.1	—	39.53	–2.6	11.1	—	—
18	Spike–high	48.0	110.15	50.8	—	28.80	–29.7	–20.9	—	—
19	Well–low	–7.3	–22.51	–29.9	—	–12.75	–2.5	17.7	—	—
20	Well–medium	–10.2	32.14	–19.5	—	–3.94	–2.1	15.8	—	—
21	Well–high	–8.7	110.15	–10.2	2.1	8.26	–6.5	18.7	12.4	6.2
22	Spike–low	44.2	–22.51	14.5	—	23.31	–7.4	8.7	—	—
23	Spike–medium	44.7	32.14	27.4	9.8	37.96	–4.1	10.2	–17.2	27.9
24	Spike–high	43.4	110.15	27.9	8.3	27.35	–27.7	–0.5	–19.0	18.9
25	Well–low	–8.9	–22.51	–27.6	–9.1	–8.74	2.9	19.4	19.0	0.3
26	Well–medium	–6.9	32.14	–22.0	—	–4.99	–5.9	17.4	—	—
27	Well–high	–9.4	110.15	–4.4	—	0.75	–13.4	5.2	—	—
28	Spike–low	44.3	–22.51	7.8	—	15.65	–14.9	7.8	—	—
29	Spike–medium	31.8	32.14	19.1	—	—	—	—	—	—
30	Spike–high	41.1	110.15	17.8	—	27.87	–25.5	9.8	—	—

Note: Food $\delta^{13}C$ was manipulated by raising larvae of *Musca domestica* on substrates labeled with lyophilized, ^{13}C-enriched algal cells. Water DIC $\delta^{13}C$ was manipulated by adding ^{13}C bicarbonate; given value is the mean of all samples taken from the individual aquarium of that fish. Isotopic enrichment factors (ε) are also given; see text for definitions and calculations. No enrichment factors were calculated for the five fish for which otolith $\delta^{13}C$ was not available. Enrichment to or from endolymph was calculated only in cases where the endolymph sample was sufficiently large to produce reliable estimates of $\delta^{13}C$.

The net isotopic enrichment between C sources and the blood was near zero or slightly negative. Based on the full model fit to $\delta^{13}C_{oto}$, ε_{total} was not significantly different from 0 ($\beta_0 = -1.8‰ \pm 1.8‰$; $t_{22} = 1.0$, $p = 0.3$). However, the reduced model (excluding all of the spike–medium and spike–high fish) yields a slightly lower estimate of ε_{total} ($-2.7‰ \pm 1.2‰$; $t_{15} = 2.2$, $p = 0.04$). Our measurements of the isotopic composition of water, food, blood, endolymph, and otolith indicated that this small net depletion in ^{13}C between C sources and the otolith is the result of countervailing depletions and enrichments at different physiological steps. There was a large depletion of ^{13}C as C moved from food and water sources into the blood ($\varepsilon_{blood-sources} = -16.9‰ \pm 1.1‰$, $n = 23$; excludes two extreme outliers). In contrast, movement of C from the blood into the otolith resulted in ^{13}C enrichment ($\varepsilon_{oto-blood} = 13.3‰ \pm 1.3‰$, $n = 23$; excludes two extreme outliers). The sum of these two enrichment terms, which represents the net enrichment term from sources to otolith, is in fairly close agreement with the model estimate of this net enrichment. Because only 11 endolymph samples were sufficiently large to produce good estimates of $\delta^{13}C$, we can make only a crude estimate of the relative contribution of $\varepsilon_{endo-blood}$ ($13.2‰ \pm 2.4‰$, $n = 11$) and $\varepsilon_{oto-endo}$ ($-2.5‰ \pm 2.0‰$, $n = 8$; excludes otolith outliers) to the total enrichment between blood and otolith. Nonetheless, these estimates indicate that most of the enrichment is associated with the blood-to-endolymph step, especially since $\varepsilon_{oto-endo}$ is not significantly different from 0 ($t_7 = 1.3$, $p = 0.2$).

Discussion

Sources of otolith C

The information stored in otolith C isotope records is of limited utility unless the sources of otolith C are known. To this end, several authors have attempted to estimate *M*, the proportion of metabolically derived C in the otolith. Often, however, the $\delta^{13}C$ of water DIC and food end members was poorly controlled or even unknown in these studies. Therefore, it is difficult to assess whether the wide range in esti-

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Fig. 2. Response of otolith $\delta^{13}C$ to experimental manipulations of carbon isotope ratio of food and water end members. Mean $\delta^{13}C$ (±1 standard error) of water (solid circles) and food (open circles) end members for each water–food treatment combination (well, unaltered well water; spike, well water spiked with $NaH^{13}CO_3$; low, unlabelled food; med, 2 g labelled food; high; 4 g labelled food) are plotted, along with otolith values for each fish (solid triangles).

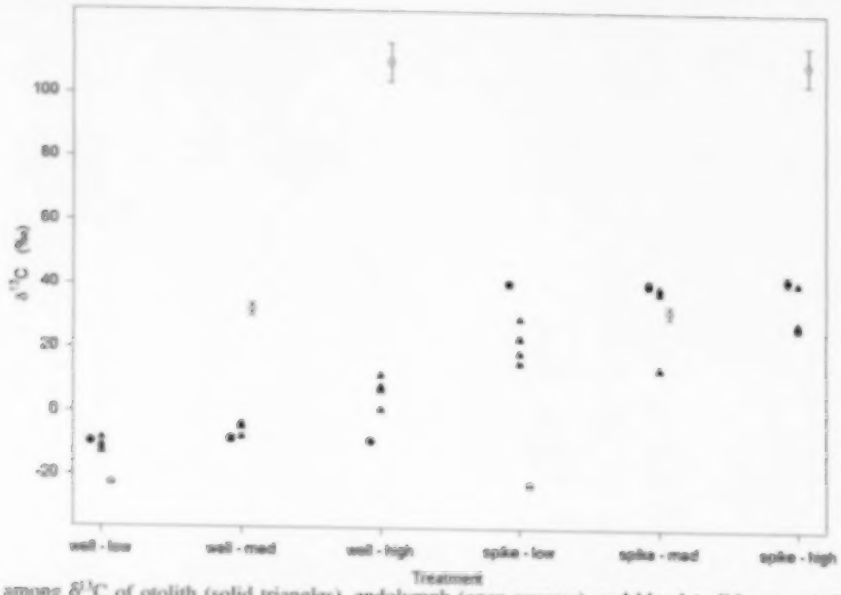
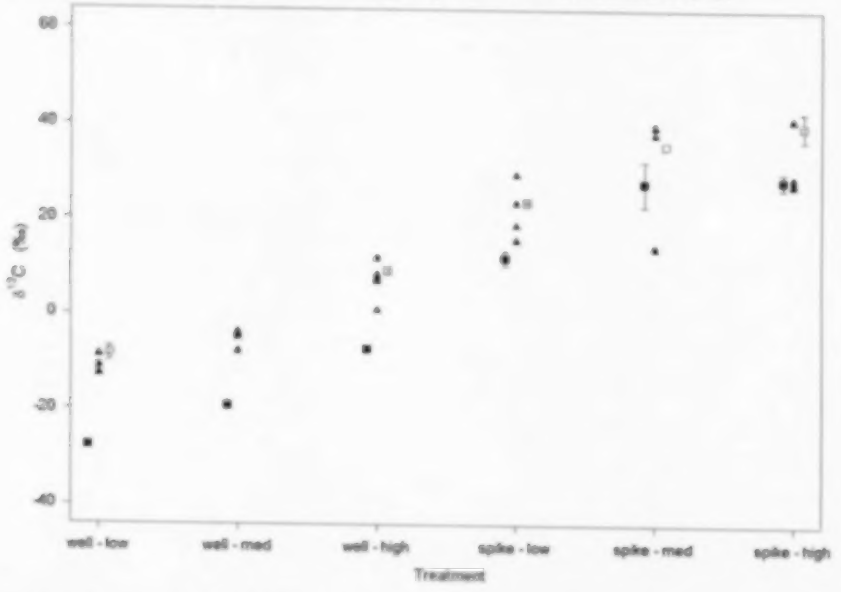


Fig. 3. Relationship among $\delta^{13}C$ of otolith (solid triangles), endolymph (open squares), and blood (solid squares). Mean $\delta^{13}C$ (±1 standard error) blood and endolymph for each water–food treatment combination (well, unaltered well water; spike, well water spiked with $NaH^{13}CO_3$; low, unlabelled food; med, 2 g labelled food; high; 4 g labelled food) are plotted, along with otolith values for each fish. Endolymph data are plotted only where samples were large enough to produce reliable estimates of $\delta^{13}C$.



mates of M (Table 2) reflects natural variability. In the present study, we directly manipulated and repeatedly measured the stable C isotope ratios of both food and water end members. By creating large differences in end member $\delta^{13}C$, we were able to construct a well-constrained mixing model to solve for M. We determined that $M = 0.17$ for juvenile rainbow trout under laboratory conditions. The remaining 83% of otolith C derives from dissolved inorganic C in the water.

How does all this C get from the water into the otolith? One of the first studies to deduce the large contribution of ambient DIC to the otolith concluded that access from water

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Table 2. Selected estimates of *M* (the proportion of otolith carbon that is metabolically derived).

Study	Type	System	Species	$\delta^{13}C_{water}$	$\delta^{13}C_{food}$	*M*	Fish age or size
Radtke 1984	expt	m	*Mugil cephalus*	Estimated	Not measured	>0	
Kalish 1991*a*	obs	m	Many	Estimated	Not measured	>0	
Kalish 1991*b*	expt	m	*Arripis trutta*	Estimated	Estimated	0.32–0.35	Juvenile (45–70 mm)
Thorrold et al. 1997	expt	m	*Micropogonias undulatus*	Measured	Assumed	>0	
Schwarcz et al. 1998	obs	m	*Gadus morhua*	Not measured	Not measured	0.07–0.43	Adult to juvenile
Weidman and Millner 2000	obs	m	*Gadus morhua*	Estimated	Estimated	0.20	Adult (2–12 year)
Tohse and Mugiya 2004	expt	fw	*Carassius auratus*	NA[a]	NA[a]	0.17	Juvenile (8–12 g)
Høie et al. 2003	expt	m	*Gadus morhua*	Measured	Measured	0.28–0.32	Juvenile (≤ 20 mm)
Wurster and Patterson 2003	obs	fw	*Aplodinotus grunniens*	Considered[b]	Considered[b]	0.00–0.95 or 0.05–1.00[b]	Adult to juvenile
This study	expt	fw	*Oncorhynchus mykiss*	Measured	Measured	0.17	Juvenile (~130 mm)

Note: Expt, experimental; obs, observational; fw, freshwater; m, marine. Fish age or size is given only for studies where a value of *M* was estimated. When estimated *M* is a range of values, range of size or age is given in same order.

[a]Not applicable; Tohse and Mugiya (2004) used glucose and water dissolved inorganic carbon (DIC) labeled with ^{13}C to measure carbon incorporation by the otolith.

[b]Wurster and Patterson (2003) examined fossil otoliths. They consider the potential variability of $\delta^{13}C_{water}$, $\delta^{13}C_{food}$, and *M* and note that patterns in their data are explainable solely as a result of ontogenetic changes in *M*, assuming that *M* can change by 0.95 during the life of an individual.

to the inner ear must be hindered at most by membranes permeable to DIC (Degens et al. 1969). Two membrane-mediated mechanisms for DIC uptake seem possible: via ingestion of water and uptake across the gut or via exchange across the gills. At first glance, substantial uptake of DIC across the gut seems unlikely, as it is generally thought that active drinking by freshwater fishes is minimal because of osmoregulatory constraints. However, studies with salmonids held in fresh water have indicated a low but appreciable rate of drinking (~0.6–0.8 $mL \cdot kg^{-1} \cdot h^{-1}$; Fuentes and Eddy 1996; Fuentes et al. 1996). If fish in our experiment drank water at a similar rate, they would have ingested ~0.01 $mmol\ C \cdot day^{-1}$ as water DIC. While this rate is low compared with the ingestion of food (~20 $mmol\ C \cdot day^{-1}$), it could easily account for 83% (or even 100%) of the new C precipitated onto the otolith during the experiment. Thus, our results are consistent with the hypothesis that DIC uptake occurs across the gut, assuming that movement of ingested water DIC into the bloodstream is faster than movement of ingested food C into the bloodstream. It is also possible that water DIC enters the bloodstream via exchange across the gills; while fish respiration and osmoregulation rely on an outward gradient in C concentration across the gills (Tufts and Perry 1998), there could be substantial inward movement of DIC across the gills despite net outward flux. A general model that describes the degree of equilibration between metabolic and ambient CO_2 based on the concentration of CO_2 and O_2 in the blood relative to the ambient environment (aquatic or terrestrial) (McConnaughey et al. 1997) reaches a similar conclusion. Further work is necessary to determine the relative magnitude of DIC uptake across the gut versus across the gills.

Our estimate of *M* is lower than many previously published estimates (Table 2). There are several potential explanations for this observation. First, since most studies of sources of otolith C have used marine fishes, it is possible that differences between marine and freshwater fishes dictate a lower contribution of metabolic C to otoliths in freshwater fishes. Indeed, the only other source determination for otolith C from a contemporary freshwater fish (Tohse and Mugiya 2004) reported $M = 0.17$, identical to the value we found. We can think of no physiological mechanism that would lead to greater metabolic contributions to otolith C in marine fishes. If anything, the osmoregulatory necessity of constant drinking in the marine environment would be expected to increase the amount of water DIC in the bloodstream, thereby lowering *M*. It is possible that the high DIC in the water in this study (~6 $mmol \cdot L^{-1}$) compared with typical marine DIC (~2 $mmol \cdot L^{-1}$) increased the influx of C across the gills, lowering *M*. Again, the physiological mechanism that would produce such a result is unclear to us. We conclude that marine–freshwater differences are unlikely to explain the patterns in *M* shown in Table 2. Another possible explanation for the low value of *M* that we observed relative to other studies is the age or size of the fish in our study. Several authors have suggested that since the metabolic rate of fishes generally decreases with age, metabolic contributions to otolith C should also decline (Mulcahy et al. 1979; Kalish 1991*a*; Schwarcz et al. 1998). Our estimate of $M = 0.17$ for juvenile (fork length ~130 mm) trout is lower than estimates for very young *Arripsis trutta* ($M = 0.32–0.35$ at

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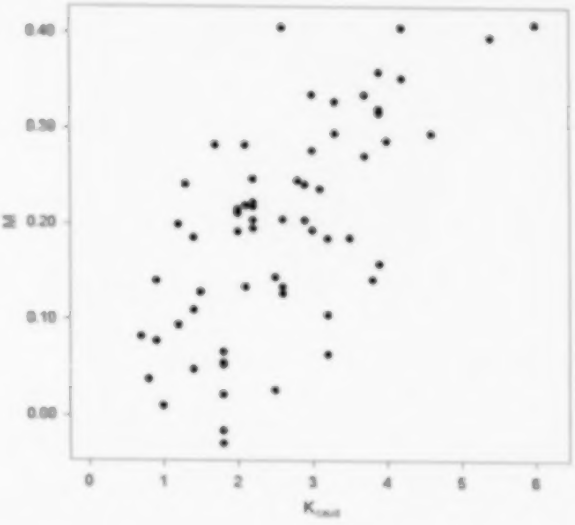
45–70 mm) and *Gadus morhua* (M = 0.28–0.32 at <20 mm), but higher than some estimates for adult fish (e.g., *G. morhua*, M = 0.07 for age 12 fish) (Table 2). On the other hand, there are clear exceptions to this pattern; for example, another study of adult *G. morhua* reported M = 0.20, similar to what we measured for juvenile trout.

A model that relates otolith $\delta^{13}C$ to total (active + standard) metabolism (Sherwood and Rose 2003) could explain both the general trend of decreasing M with increasing age and the considerable variation around this relationship. Total metabolic rate (which determines M, the proportion of metabolic C in the blood and otolith) depends strongly on activity more than on standard metabolic rate (SMR; Sherwood and Rose 2003). All fishes generally exhibit decreasing SMR with age; this explains the trend of decreasing M with increasing age. However, differences in activity across species or ontogenies will introduce considerable variation around this relationship between SMR and age. Sherwood and Rose (2003) demonstrated that caudal aspect ratio (K_{caud}, a morphometric index of swimming activity) is a uniquely strong predictor of otolith $\delta^{13}C$. We used their data to calculate M for 63 of the 67 marine fish species that they consider and examined the relationship between M and K_{caud} (Fig. 4). The best fit regression line for these data is $M = 0.025 + 0.066K_{caud}$; $R^2 = 0.45$, $p < 0.0001$. Using this equation and assuming that the value given for K_{caud} of *Oncorhynchus nerka* (2.6; Sherwood and Rose 2003) is a close approximation to K_{caud} of *O. mykiss*, we calculated that M should equal 0.19 for fish in the present study. This is in very close agreement with our empirical estimate, M = 0.17. Besides increasing the proportion of metabolically derived C in the bloodstream, short-term changes in activity may change the isotopic composition of this C. Gauldie (1996) suggested that high metabolic loads reduce discrimination against ^{13}C as available food resources are more "fully oxidized"; this might occur if utilization of carbohydrates increases relative to lipids, which are isotopically light (DeNiro and Epstein 1978). A similar phenomenon is known to occur in humans (Panteleev et al. 1999). The total metabolism model of Sherwood and Rose (2003) shows considerable promise as a means of understanding the effects on otolith $\delta^{13}C$ of changes in metabolic rate at short and long temporal scales. Future efforts to explicitly parameterize this model via controlled studies may greatly increase our ability to explain and predict patterns in otolith $\delta^{13}C$.

Fig. 4. Proportion of otolith carbon (C) that is metabolically derived (M) plotted against caudal aspect ratio (K_{caud}) for 63 species of marine fish, based on data in Sherwood and Rose (2003). We calculated M using the equation $\delta^{13}C_{oto} = M\delta^{13}C_{blood} + (1 - M)\delta^{13}C_{water}$. $\delta^{13}C_{blood}$ was calculated from estimated $\delta^{13}C$ of pelagic and benthic prey and species-specific estimates of the percentage of pelagic prey in the diet (Sherwood and Rose 2003). We assumed, as did Sherwood and Rose (2003), that $\delta^{13}C_{water}$ = 0‰ for all species and used the K_{caud} and mean $\delta^{13}C_{oto}$ that they presented for each species. Four species considered by Sherwood and Rose (2003) were excluded from this analysis because of unavailable data.



Isotopic enrichment factors

Our measurements of blood $\delta^{13}C$ in this experiment indicate that blood C is considerably depleted in ^{13}C relative to a mixture of food and water sources of C ($\varepsilon_{blood-sources}$ = 16.9‰ ± 1.1‰). We were surprised by the magnitude of this depletion, since a pilot study in 2000 (which sampled blood after caudal transection rather than by cardiac puncture as in the present study) indicated little or no discrimination against ^{13}C between sources and blood (P. Weber, unpublished data). Nonetheless, the depletion that we observed was very consistent, and we assume that this result is real. It seems unlikely that much of the discrimination against ^{13}C could occur along the food-to-blood pathway. Given that observed C isotope enrichment between a consumer's diet and its tissues is usually on the order of 0‰–1‰ (DeNiro and Epstein 1978; Vander Zanden and Rasmussen 2001), and since there must be a net isotopic balance between ingested food and the incorporated, respired, and egested portions of that food, there is little scope for negative values of $\varepsilon_{endo-blood}$. Most of the isotopic fractionation must therefore occur along the pathway from water DIC to blood. The vast majority of the DIC that moves inward across the gut or the gills is probably in the form of dissolved CO_2, given that these membranes are considerably more permeable to CO_2 than to HCO_3^-. Dissolved CO_2 is ~8‰–9‰ lighter than HCO_3^- because of equilibrium fractionation of isotopes between these C species (Emrich et al. 1970; Zhang et al. 1995). Because essentially all DIC was HCO_3^- in our study (pH = 8.2), the stable isotope analysis of bulk water indicates $\delta^{13}C$ ~8‰–9‰ heavier than the C that is likely to move from the water into the fish. This explains about half of the estimated $\varepsilon_{blood-sources}$. The remainder may be explained by a kinetic mechanism, whereby faster reaction kinetics for molecules containing ^{12}C increase the proportion of ^{12}C relative to ^{13}C in the product of the reaction. Such kinetic effects could occur either as CO_2 diffuses inward across the gut or gills or during the $CO_2 \rightarrow HCO_3^-$ reaction, as long as the product of the reaction is removed from the reaction site faster than the rate of back reaction.

Even more surprising than the considerable discrimination against ^{13}C as C moves from the water across the gut or gills and into the bloodstream is the considerable enrichment in

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^{13}C as C moves from the bloodstream into the endolymph ($\varepsilon_{endo-blood}$ = 13.2‰ ± 2.4‰). Based on existing models for the transport of C into the sacculus (Payan et al. 1997; Tohse and Mugiya 2001), there is no obvious mechanism for such considerable ^{13}C enrichment. Active transport of HCO_3^- is important in the movement of C from the blood across the cells of the saccular epithelium to the endolymph (Tohse and Mugiya 2001). However, this transport mechanism is not expected to result in ^{13}C enrichment. The results of the present study suggest two hypotheses: (*i*) active transport of HCO_3^- favors $H^{13}CO_3^-$ and (*ii*) there is a significant outflow of C from the sacculus to the blood that favors ^{12}C. While these hypotheses are not mutually exclusive, it is likely that outflow would be necessary to produce the large ^{13}C enrichment that we measured. Carbonic anhydrase, an enzyme that speeds the $CO_2 \leftrightarrow HCO_3^-$ equilibration, has been shown to play an important role in C transport into the sacculus (Tohse and Mugiya 2001). This enzyme potentially could play a role in establishing an 8‰–9‰ difference in $\delta^{13}C$ between CO_2 diffusing to the blood and the HCO_3^- transported to the endolymph. Enrichment of the endolymph DIC relative to the blood DIC would be a function of transport rates. Clearly, further work is necessary to ascertain the magnitude and mechanisms of isotopic fractionation between C sources and C in the blood and endolymph.

Implications for applied studies of otolith $\delta^{13}C$

Because both the prey consumed and the $\delta^{13}C$ of that prey may vary considerably between individual fish and across time and space, efforts to constrain the isotopic signature of this end member are often difficult and expensive at best. Fortunately, our results indicate that efforts to interpret otolith $\delta^{13}C$ data may often be adequately constrained solely by measuring patterns in water DIC $\delta^{13}C$, without regard to the $\delta^{13}C$ of consumed prey. For instance, as juvenile Chinook salmon (*Oncorhynchus tshawytscha*) outmigrate from the Sacramento – San Joaquin system in California, there is considerable variation in the $\delta^{13}C$ of their gut contents (approximately –20‰ to –26‰, n = 150; P. Weber and C. Solomon, unpublished data). There is also a steady decrease in water DIC $\delta^{13}C$, from about –6‰ in large tributaries to about –9‰ in the Sacramento – San Joaquin Delta (Finlay 2003; P. Weber, unpublished data). If water DIC makes up 83% of otolith C in these salmon, back-of-the-envelope calculations indicate that we can accurately resolve time spent in headwaters from time spent in the Delta based on retrospective analyses of otolith $\delta^{13}C$ and knowledge of water DIC $\delta^{13}C$ in these habitats, regardless of likely variation in food $\delta^{13}C$. The ability to resolve habitat use is fairly robust to variation in M, unless there is a substantial and directional change in M that counterbalances the trend in DIC $\delta^{13}C$. Furthermore, large spatial gradients in DIC $\delta^{13}C$ are common in a variety of aquatic systems, including with depth (Schwarcz et al. 1998) or across barriers to flow (Dufour et al. 1998) in the ocean and longitudinally in lake–river–estuary systems (e.g., Northcote et al. 1992; the Sacramento – San Joaquin system). Thus, efforts to infer fish movement patterns from otolith C isotopes may often require only moderately constrained estimates of M and DIC $\delta^{13}C$. In cases where more precise resolution is required, detailed consideration of variation in M will likely be necessary. As we have suggested, a model relating total metabolism to otolith $\delta^{13}C$ (Sherwood and Rose 2003) provides a strong unifying framework for such analyses. Future refinement of our understanding of sources of otolith C may focus on more explicit parameterization of this model with respect to taxonomy, ontogeny, habitat, and other factors. Controlled manipulations of the isotopic composition of food and water end members will be an essential tool for this research.

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How does the European eel (*Anguilla anguilla*) retain its population structure during its larval migration across the North Atlantic Ocean?

A. James Kettle and Keith Haines

Abstract: A Lagrangian model is presented of the current-carried migration of the leptocephali (larvae) of the European eel (*Anguilla anguilla*) across the North Atlantic Ocean from the spawning area in the Sargasso Sea to the adult range in Europe and North Africa. The success of larvae in crossing the Atlantic Ocean and reaching particular latitude bins on the eastern side depended strongly on starting location in the Sargasso Sea and migration depth. In the model domain, silver eel spawners can develop strategies for spawning location and migration depth to preferentially target particular regions in the adult range. This observation may help to explain the presence of gradients in molecular markers in eel samples collected across Europe. Spawning in the period of late winter – spring maximizes the average food availability along the 2-year larval trajectory. The fastest transatlantic larval migration in the model is about 2 years, and the route to Europe takes most of the larvae past the east coast of North America in the first year. These model results are consistent with the hypothesis that the European and American eel (*Anguilla rostrata*) could separate themselves on different sides of the Atlantic Ocean on the basis of the different durations of their larval stages.

Résumé : Nous présentons un modèle lagrangien de la migration sous l'effet des courants des larves leptocéphales de l'anguille d'Europe (*Anguilla anguilla*) à travers le nord de l'Atlantique depuis les sites de reproduction dans la mer des Sargasses vers les aires de répartition des adultes en Europe et en Afrique du Nord. Le succès de la traversée de l'Atlantique par les larves et leur atteinte de créneaux particuliers de latitudes sur la rive est dépendent fortement de leur point de départ dans la mer des Sargasses et de la profondeur à laquelle elles migrent. Dans le domaine du modèle, les anguilles argentées reproductrices peuvent mettre au point des stratégies impliquant le site de reproduction et la profondeur de migration afin de cibler de façon préférentielle des régions particulières de l'aire de répartition des adultes. Cette observation peut aider à expliquer l'existence de gradients dans les marqueurs moléculaires dans les échantillons d'anguilles prélevés du bout à l'autre de l'Europe. Une reproduction en fin d'hiver et au printemps maximise la disponibilité moyenne de nourriture le long de la trajectoire de 2 ans des larves. La migration larvaire transatlantique la plus rapide dans le modèle dure environ 2 ans et la route vers l'Europe amène la plupart des larves au large de la côte est de l'Amérique du Nord durant la première année. Ces résultats de la modélisation s'accordent bien avec l'hypothèse qui veut que les anguilles d'Europe et d'Amérique (*Anguilla rostrata*) se séparent en direction de côtes différentes de l'Atlantique d'après les durées distinctes de leurs stades larvaires.

[Traduit par la Rédaction]

Introduction

It is remarkable that the European eel (*Anguilla anguilla*) may retain regionally distinct population structure (e.g., Daemen et al. 2001; Wirth and Bernatchez 2001; Maes and Volckaert 2002) during a life cycle that incorporates two migrations across the North Atlantic Ocean at the beginning and end of its life (e.g., Tesch 2003). The mature silver eel leaves the rivers of Europe and North Africa in the autumn and swims across the North Atlantic Ocean (navigating by an unknown process) to spawn in the Sargasso Sea in the first half of the following year. Although the spawning process has never been observed, the small eel larvae (leptocephali) appear in the Sargasso Sea between February and July and drift on the ocean currents (Schmidt 1923; McCleave et al. 1987; see Fig. 1 for the locations of reported captures) back to the normal adult range in Europe and North Africa (Schmidt 1909; Dekker 2003). This passive migration on the ocean currents is particularly problematic because the North Atlantic Ocean is characterized by a vigorous eddy field that might serve to confound any long-distance migration strategy based on passive drift of an extended larval stage

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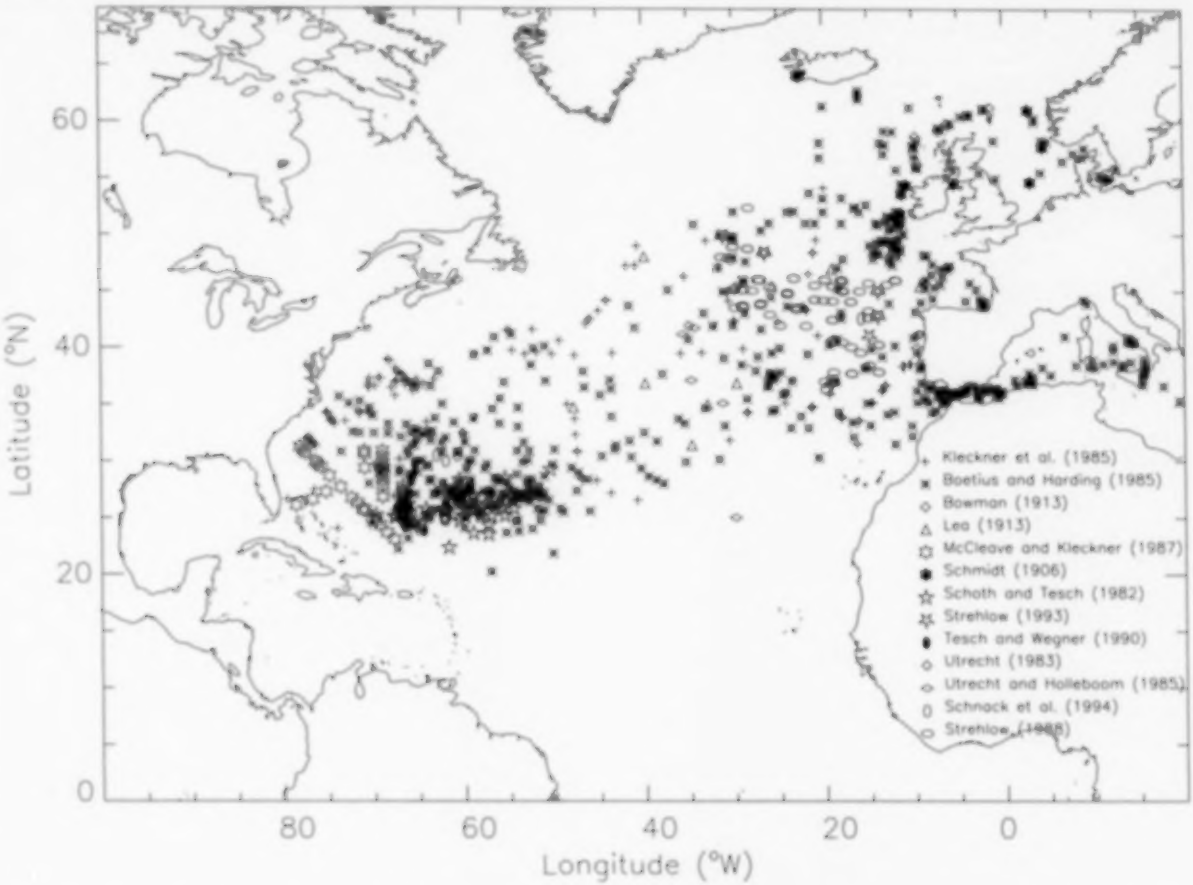
Fig. 1. Database of locations of larval (leptocephali and metamorphosing glass eels, *Anguilla* spp.) captures from Schmidt (1906); Bowman (1913); Lea (1913); Schoth and Tesch (1982); van Utrecht (1983); Boetius and Harding (1985); Kleckner et al. (1985); van Utrecht and Holleboom (1985); McCleave and Kleckner (1987); Kleckner and McCleave (1988); Strehlow (1988); Tesch and Wegner (1990); Strehlow (1993); and Schnack et al. (1994).



(McCleave 1993; Cowen et al. 2000; McCleave 2003). The link between the Sargasso Sea spawning region and the adult range seems tenuous, but molecular marker studies suggest that there may be a reliable mechanism for population segregation during the two migrations across the North Atlantic Ocean. In the present study, we report the results of a series of Lagrangian studies in which we show how larvae starting in the Sargasso Sea may not be randomized during their migration across the North Atlantic Ocean but may develop strategies to maximize their chances to arrive in certain regions of Europe and North Africa.

Materials and methods

This Lagrangian study is based on experimental circulation fields that have been generated through a data-assimilation exercise based on the Ocean Circulation and Climate Advanced Modelling (OCCAM; http://www.soc.soton.ac.uk/JRD/OCCAM) Project global oceanic circulation model to generate possibly the most accurate and complete picture of ocean circulation for the period 1993–1996 (Fox and Haines 2003) currently available. The model was run on a one-quarter degree latitude–longitude grid with 36 depth levels and was forced with 6-hourly wind stress data from the European Centre for Medium Range Weather Forecasts (http://www.ecmwf.int) operational analysis. The assimilation of expendable bathythermograph temperature profiles at 30-day intervals and TOPEX/Poseidon satellite altimetry data at 10-day intervals into this model prevents the drift of model temperature and currents away from real-world values (see Fox and Haines 2003 for more details).

The Lagrangian study was based on 5-day average circulation fields (archived at www.nerc-essc.ac.uk/godiva). The Lagrangian investigation entailed the release of virtual drifters in the Sargasso Sea in a rectangle enclosing the most probable spawning regions of the European and American (*Anguilla rostrata*) eel, determined by McCleave et al. (1987) on the basis of numerous reports of captures. Within this region, the drifters were released at 1° latitude–longitude intervals daily for 2 years at a range of depths in the uppermost 750 m of the model. Drifters were not permitted to change depth during the migration according to horizontal

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convergence–divergence criteria, as there is evidence that the real larvae have buoyancy control and can maintain a constant average depth station in the water column (i.e., when the diurnal vertical migration is averaged over a 24 h period; Schoth and Tesch 1983). Although field studies have indicated that the silver eel has particular spawning strategies for time and location and also for migration depth, an unbiased release strategy was chosen to see if the model could predict features of the reproduction strategy adopted by the organism among the various possibilities available. The Lagrangian approach used here is similar to the procedure used by Harden Jones (1968) for the larval migration from the Sargasso Sea to Europe and by Fricke and Kaese (1995) for the silver eel migration from Europe back to the Sargasso Sea. However, the data-assimilation circulation fields of the present study are more accurate and better resolved than those of the earlier studies, and a greater range of parameter space (for location and time of spawning and depth of migration) is investigated.

The trajectories were stepped forward using an iterative semi-implicit method that employed a variable time step determined to produce a 2 km horizontal displacement. Because only 4 years of ocean circulation data were available for the investigation and the full larval life span is about 2 years (Schmidt 1923; Harden Jones 1968), it was decided to release eel tracers regularly during the first 2 years and to follow each tracer for a period of 2 years. The first of the daily drifter releases was therefore terminated on the first day of the third year and last of the daily drifter releases in the second year was terminated on the last day of the fourth year. This release and tracking strategy utilized the full temporal information contained in the 4 years of archived circulation field data. To obtain enough trajectory arrivals after a 2-year travel time to perform a statistical analysis, the finishing line for a successful transatlantic migration was moved westward from the edges of the continental shelves of Europe and Africa. It was assessed as the first eastward crossing of the 25°W meridian rather than the arrival of the drifters on the coasts of Europe and North Africa. The 25°W meridian was chosen arbitrarily as a finishing line on the eastern side of the North Atlantic Ocean that does not intersect continents (where larvae could not be advected) or continental shelf regions (where larvae depend on a tidal transport mechanism not available from the model).

Results

Starting in the Sargasso Sea, the larvae were able to make the full transatlantic journey (i.e., crossing the 25°W meridian) to reach all latitudes of the adult range in Europe and North Africa (Fig. 2). Of 1.6×10^6 drifters released evenly in space and time in the identified spawning area, 0.66% (i.e., 8600, without accounting for predation losses) arrived at 25°W within 2 years. The trajectories indicate that the larvae were able to reach the coasts of Iceland, Ireland, United Kingdom, northwestern Spain, and Morocco within the 2-year time frame, and this is consistent with a 22-month migration between the spring spawning period and the peak in glass eel (post-leptocephalus stage) ascent of rivers on the Atlantic coast of France in January (Desaunay and Guerault 1997). The larval arrivals are not distributed evenly over all latitudes of Europe and North Africa but tend to concentrate (see Fig. 3) in the 45°N–50°N latitude band, which is consistent with the location of the largest glass eel fisheries in northern Spain, Atlantic France, and in the Severn River in England (Dekker 2003).

The location of the Lagrangian trajectories matches well with the location of previous larval captures (shown in Fig. 1), but there are some interesting differences between the capture database and the Lagrangian trajectories. The presence of larval captures without trajectories in the North Sea and the Mediterranean Sea suggests that more than 2 years may be required to reach these locations, but at this advanced stage in the larval life cycle, the migration strategy may be modified to take account of tidal currents (e.g., in the Straits of Gibraltar; McCleave et al. 1998). The model also predicts some unexpected larval routes across the North Atlantic. For example, some trajectories pass through the Caribbean Sea and the Gulf of Mexico via the Mona and Sombrero passages at 25–130 m depth before passing through the Florida Straits and continuing on across the Atlantic Ocean. This migration route has previously been recognized for the American eel on the basis of a few larval captures (McCleave and Kleckner 1987), but this is the first indication that it might also be a migration route for the European eel. Other routes pass from the Sargasso Sea to equatorial Africa along the North Equatorial Counter Current.

The profile of successful larval arrivals was analysed to find the location of origin in the Sargasso Sea, the migration depth, and the spawning month, all of which may have formed the genetic basis for selection. The starting location in the Sargasso Sea of the successful larvae has been subdivided by the 10 latitude bins at which they eventually arrive at 25°W after they cross the Atlantic Ocean (Fig. 4). Most of the larvae successfully arriving in northern Europe (40°N–60°N) start in the western region of the Sargasso Sea close to the Gulf Stream, which they use as the main migration path across the Atlantic Ocean. Larvae that eventually reach southern Europe or North Africa (25°N–40°N) may also start in the western part of the spawning zone in the Sargasso Sea, but there is a large proportion that originates in the northeast corner of the spawning zone. Larvae reaching equatorial Africa (0°N–15°N) start in the southeast corner, and no larvae reach the region between 15°N and 25°N.

The migration depths followed by the successful larvae are shown in frequency histograms (Fig. 5; for these diagrams, only the drifter releases within the *A. anguilla* spawning polygon — see Figs. 2 and 4 — were considered and not all of the releases in the full rectangle enclosing both the *A. anguilla* and *A. rostrata* spawning regions). To reach all parts of northern Europe and North Africa, the larvae travelled mostly between 50 and 400 m depth, and the mode in most of the distributions occurs at about 200 m depth. The distributions for the northernmost latitude bins are skewed slightly toward shallower trajectories, but almost no successful trajectories were located in the uppermost model layer within the wind-driven transport zone.

The issue of a preferred spawning season was initially not resolved by histogram analysis of the trajectory arrivals. The profiles of the successful *A. anguilla* arrivals (shown in Fig. 2) were integrated to create histograms of the number of successful arrivals for each month and latitude bin. The re-

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Fig. 2. Trajectories of the eel (*Anguilla anguilla*) larvae successfully crossing 25°W longitude within 2 years. The locations of larval captures are given by + symbols. The trajectories have been coloured according to the age after the release in days within the area delimited by the polygon in the Sargasso Sea (McCleave et al. 1987).

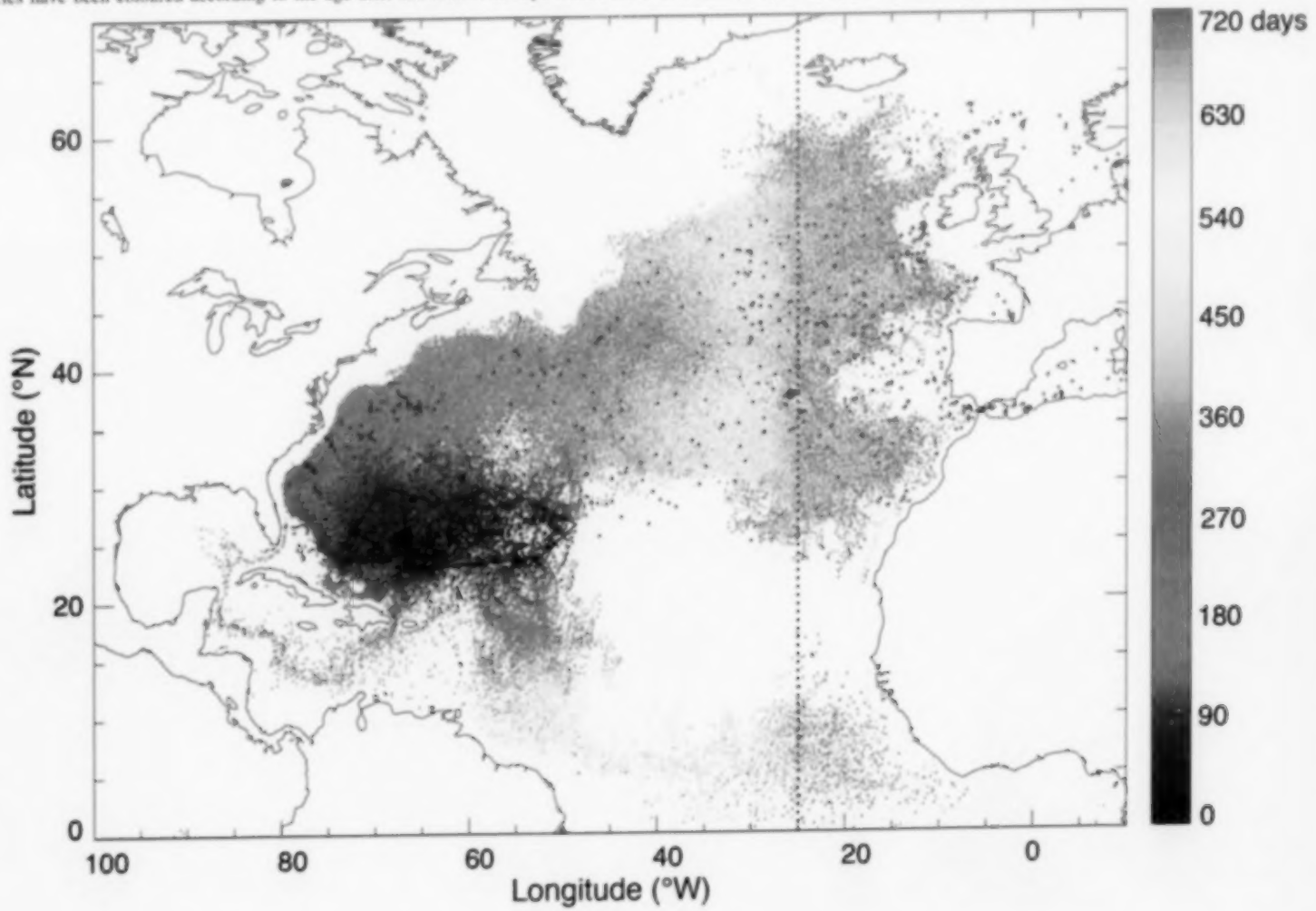

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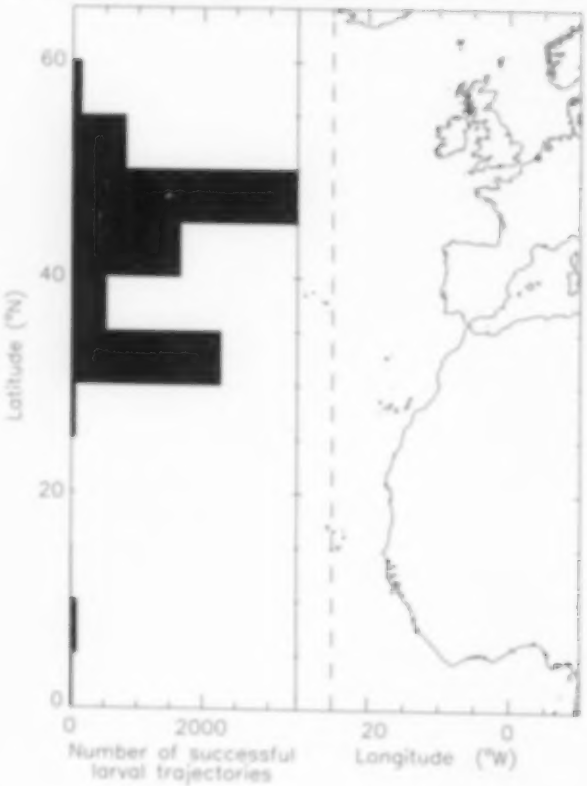
Fig. 3. Numbers of eel (*Anguilla anguilla*) larvae successfully crossing 25°W longitude within 2 years after being released within the Sargasso Sea spawning polygon (McCleave et al. 1987). The successful arrivals have been divided by 5° latitude bins from the equator to 65°N. The map on the right hand side shows the location of the latitude bins defining the histogram and the location of the 25°W meridian, defining the success of a drifter starting in the Sargasso Sea.



sult (Fig. 6) did not reveal clear trends to explain why the organism should spawn between late February and July (e.g., see the literature summary of McCleave 1993; McCleave 2003). Some of the histograms suggest that the choice of this particular spawning interval could actually reduce the chance of migration success. There thus appears to be no regular seasonal fluctuation of ocean currents that could be used by the organism to achieve a successful trans-atlantic migration.

Possibly, there has been a selection of the spawning period between late February and July to maximize the availability of food. To test this hypothesis, monthly climatology of SeaWiFS (Sea-viewing Wide Field-of-view Sensor; http://oceancolor.gsfc.nasa.gov/SeaWiFS) chlorophyll concentration was created, and chlorophyll concentrations were extracted for each point along the drifter trajectories (Fig. 7). Average chlorophyll concentrations along the trajectory tracks were calculated for a series of different time intervals — 30, 60, 120, 365, and 730 days — from the initial release time, and these were separated according the final destination latitude bin (Fig. 8). The analysis is similar to that of Desaunay and Guerault (1997), who recreated the temperature and nutrition conditions along an estimated larval migration route across the North Atlantic Ocean toward France. As well, the monthly climatological chlorophyll concentration for the *A. anguilla* spawning region was calculated (Fig. 8). While trends are difficult to observe for latitude bins that have small numbers of trajectory arrivals (i.e., 0°N–30°N and 55°N–65°N), intermediate latitude bins from 30°N to 55°N illustrate how the organism gains advantages by spawning in early spring.

The average chlorophyll concentrations along the larval migration track in the first and second years clearly depend on the spawning month. The average chlorophyll concentrations in the first year are highest when spawning in the Sargasso Sea takes place in the second quarter (April–June) and lowest if the spawning takes place in the fourth quarter (October–December). In some respects, the findings are unexpected because for a fixed location in the ocean, the calculation of the annual average of chlorophyll from a monthly climatology will not depend on the month when the calculation is started. However, because the larvae are advected from region to region, each with the different time-varying chlorophyll concentration, the annual average chlorophyll concentration depends on when the larvae start their migration in the Sargasso Sea. If chlorophyll concentration is a proxy of food availability, then the larvae would have the best availability of food if spawning takes place in the second quarter (i.e., April–June).

Interestingly, the April–June period is also the time of relatively low chlorophyll concentrations in the Sargasso Sea spawning area. It therefore appears that the organism may have chosen to maximize food availability over the first year, and this leads to a minimum in food availability in the first month of its existence. The larvae do not require much in terms of external food sources in the first month of existence but obtain nutrition from a yolk sac with oil droplets (Bertin 1956, p. 123). We speculate that since any potential predator would have to exist within the framework of an existing ecosystem based on phytoplankton primary production, the choice of introducing larvae into the Sargasso Sea at a time of low chlorophyll concentration might be part of a general predator-avoidance strategy. It is interesting to realize that the organism experiences an important hydrodynamic transition in the first 3 months of its existence when it evolves from its prelarval phase, where its environment is dominated by viscous forces, to its larval phase (Bertin 1956, p. 131), where its length enables it to swim to capture prey and avoid predators (Mann and Lazier 1991).

Discussion

The model results go some way to resolving controversy about certain aspects of the life history of the European eel. The general features of the spawning and migration strategy are broadly consistent with previous findings. However, there are also details about the spawning and migration strategies of the European eels that have not been noted in previous investigations. Moreover, by performing a large number of trajectory calculations over a full range of parameter space, it has been possible to make generalizations about how the

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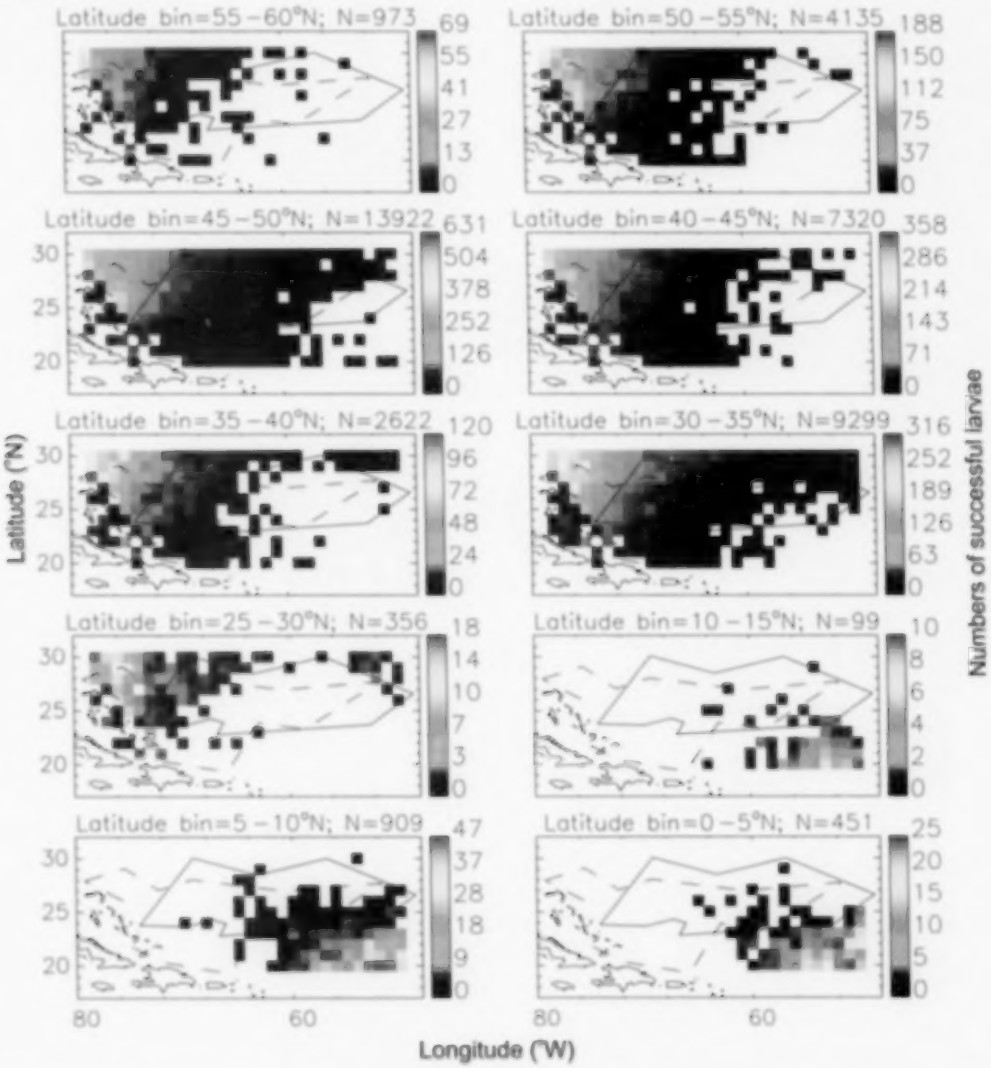
Fig. 4. Numbers of successful larvae in each latitude bin at 25°W as a function of starting location in the Sargasso Sea (colour scale). The polygons delimited by solid and dashed lines denote the spawning areas for *Anguilla anguilla* and *Anguilla rostrata*, respectively, determined by McCleave et al. (1987). For this series of model runs, the larvae were released daily at 1°×1° intervals within a box defined by 20°N–30°N latitude and 50°W–78°W longitude, but all other diagrams are based on releases from within the *A. anguilla* spawning polygon only.



population might not be homogenized during its migration across the Atlantic Ocean.

Preferred migration depth and spawning location within the Sargasso Sea

Early observational (Schmidt 1923) and modelling (Harden Jones 1968; Power and McCleave 1983) studies hypothesized that the Gulf Stream – North Atlantic Drift was the most important vehicle for the passive larval migration from the Sargasso Sea to Europe, and this has also been shown in the present work. However, the present work makes some different predictions from previous modelling studies that were based on climatological ocean current fields constructed from databases of ship drift. The problem with these derived ocean current fields was that they incorporated wind-driven Ekman currents in the uppermost 20 m of the water column. The derived currents would therefore not have been representative of the deeper ocean currents, where eel larvae have actually been captured. Tesch (2003) recognized this potential weakness in the early modelling work but could not explain why larvae were found between 50 and 400 m in the water column or why larvae would want to avoid transport in the surface layer.

The results of the present study reveal that there may be preferred migration depths that increase the overall chance of success in migrating across the Atlantic Ocean. For exam-

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Fig. 5. Depth distribution of larvae successfully crossing the 25°W meridian within 2 years after being released within the spawning polygon for *Anguilla anguilla* (shown in Figs. 2 and 4). The data have been divided according to latitude bin on the first crossing of the 25°W meridian. The vertical bars denote the range of depths of larvae captured at night (N) and during the day (D) in the North Atlantic Ocean. The diamonds and triangles respectively denote nighttime and daytime depths of larvae captured in the Sargasso Sea (Tesch 2003).

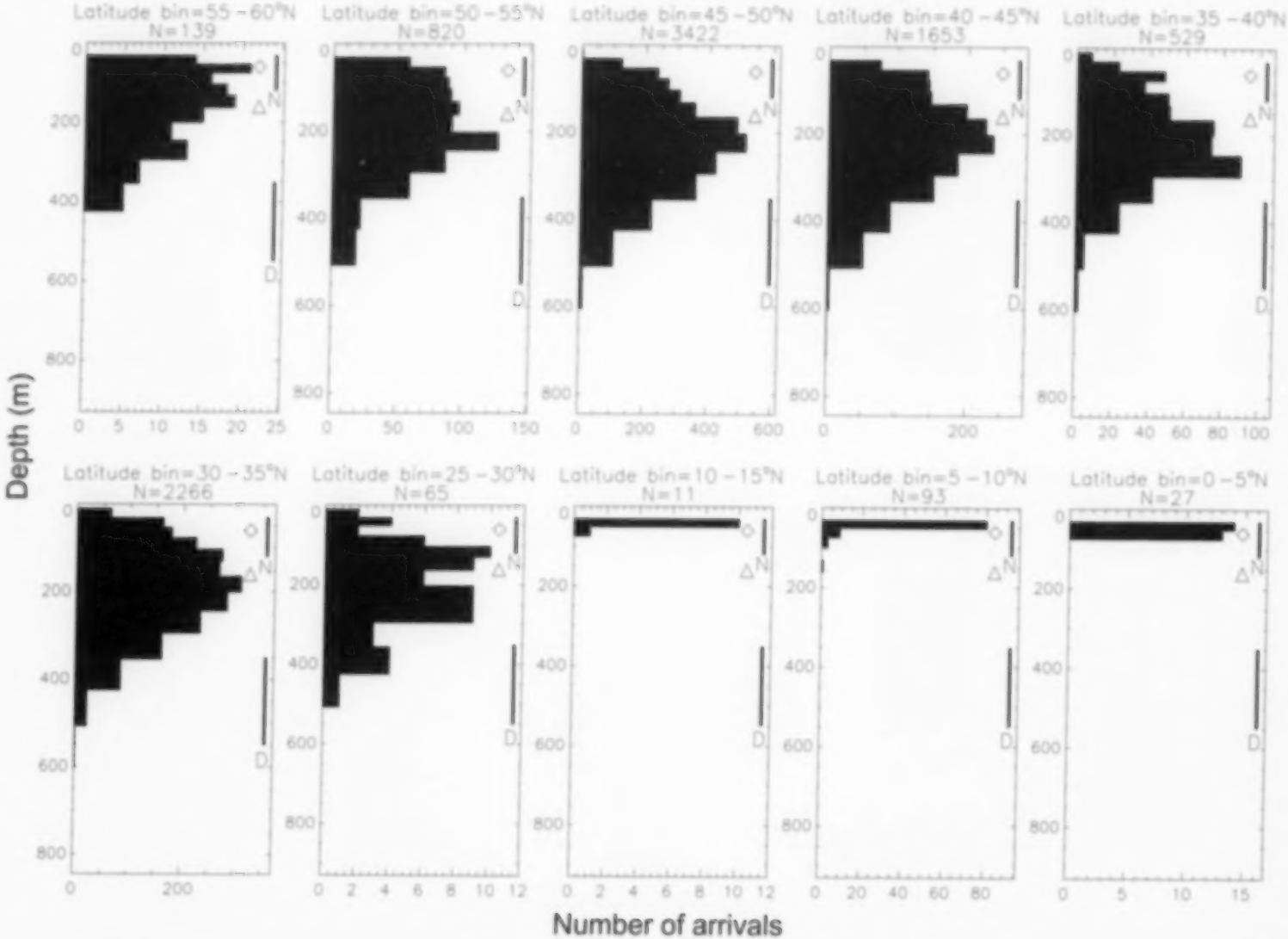

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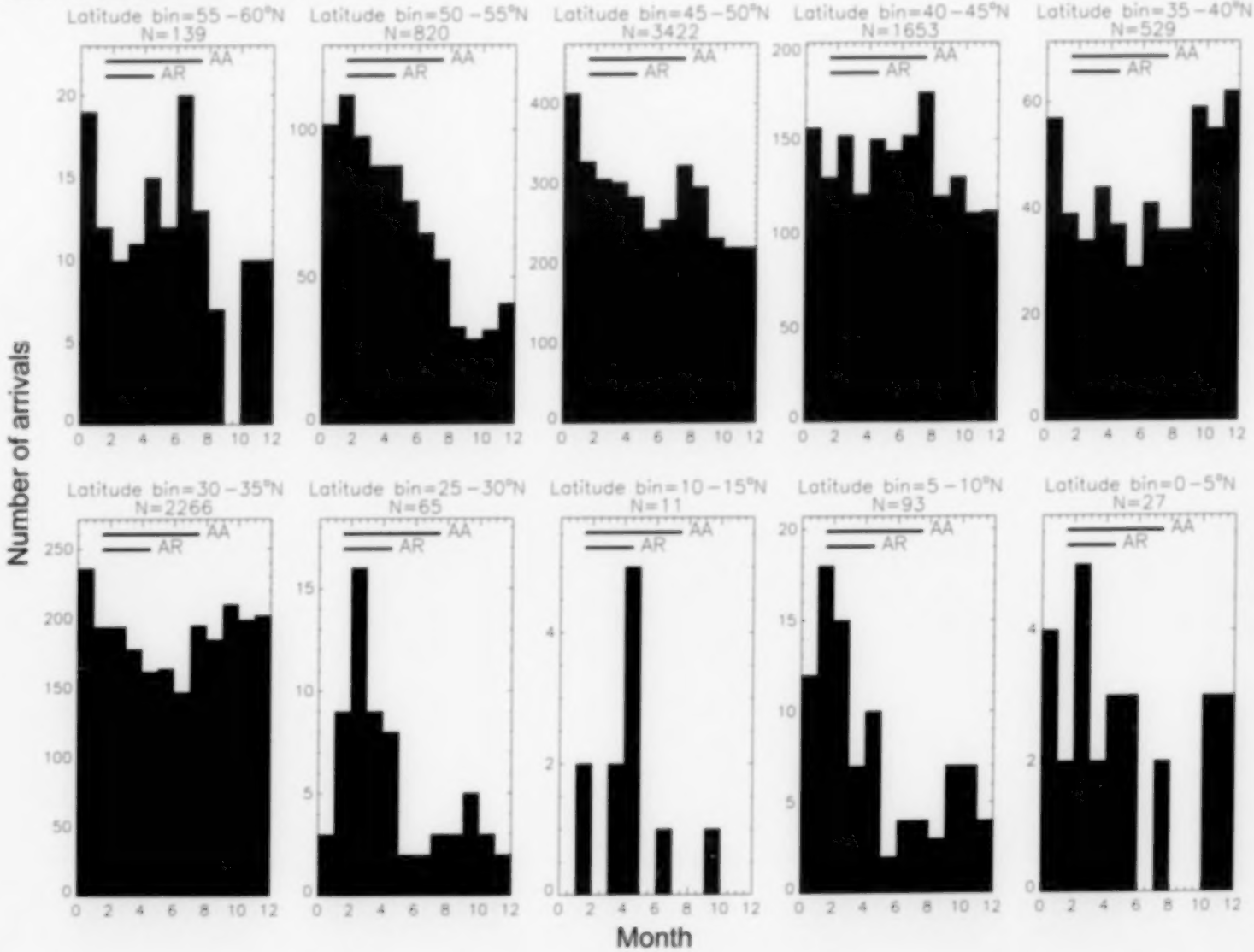
Fig. 6. Monthly distribution of larvae successfully crossing the 25°W meridian within 2 years after being released within the spawning polygon for *Anguilla anguilla* (shown in Figs. 2 and 4). The data have been divided according to latitude bin on the first crossing of the 25°W meridian. The horizontal bars denote the observed spawning periods for *A. anguilla* (AA) and *Anguilla rostrata* (AR).



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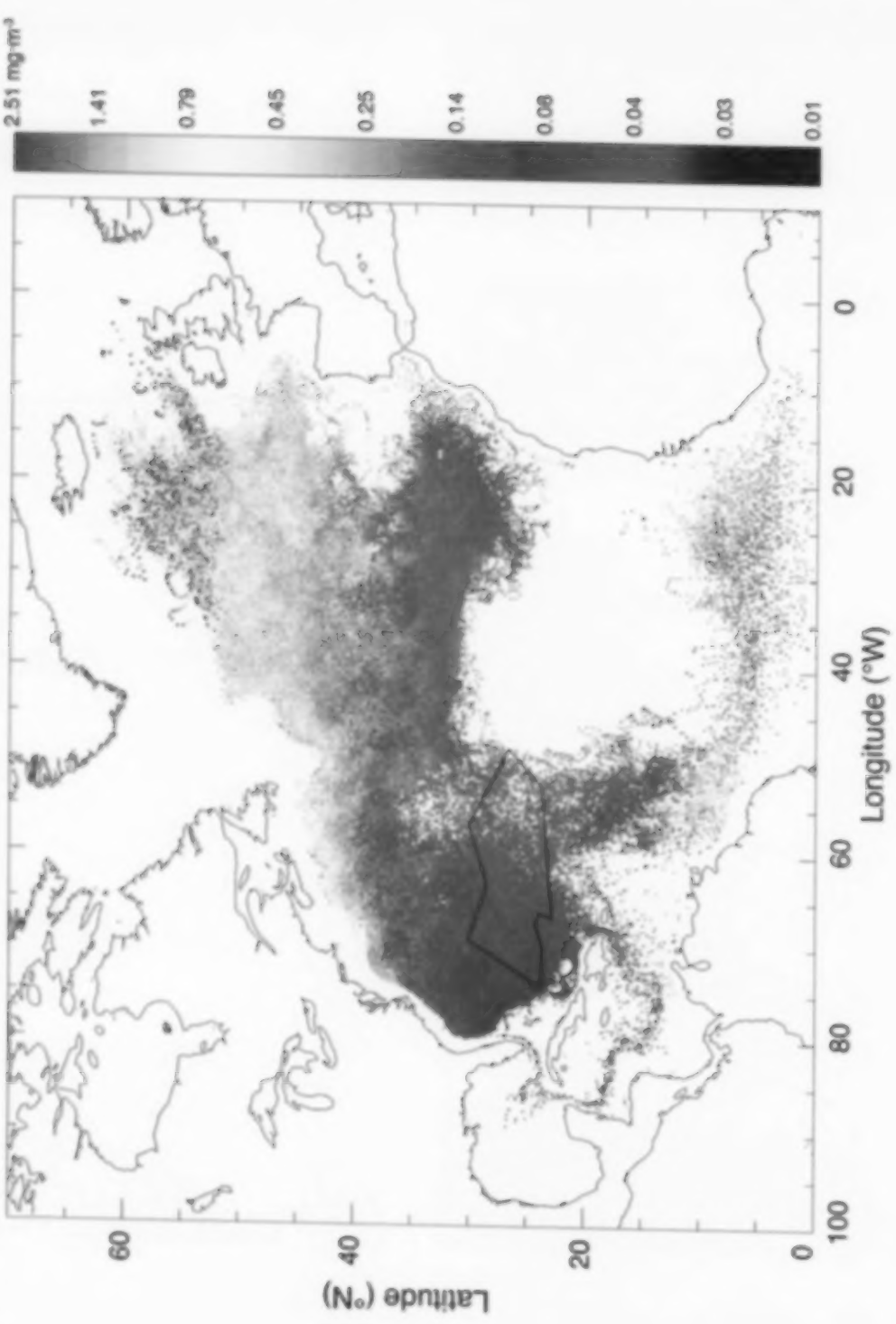

Fig. 7. Trajectories of the eel larvae successfully crossing 25°W longitude within 2 years after release within the *Anguilla anguilla* spawning polygon (McCleave et al. 1987). The trajectories have been coloured according to the monthly, climatological SeaWiFS chlorophyll concentration, with black pixels denoting missing data.

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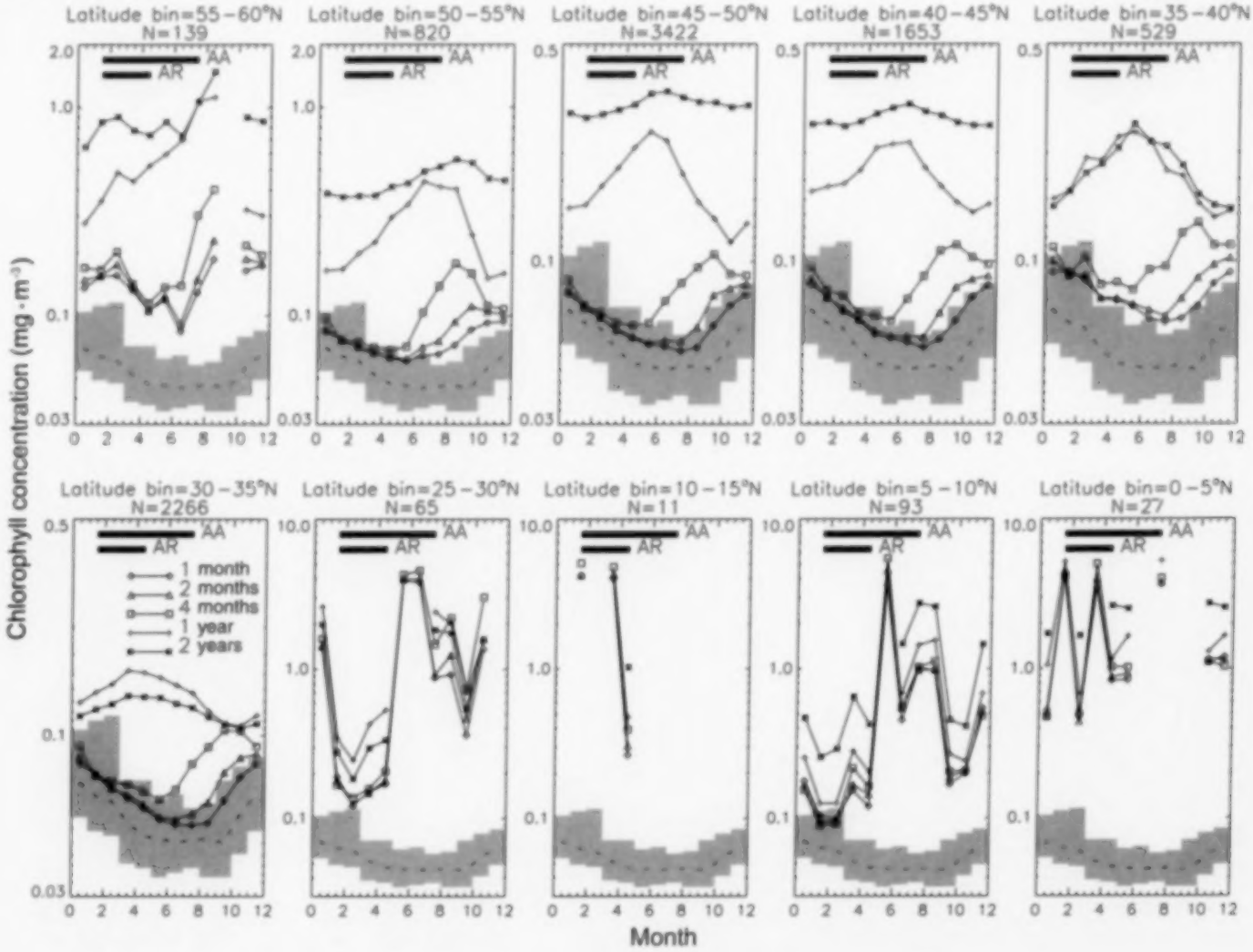
Fig. 8. Chlorophyll concentrations averaged over different time intervals (of the first 30, 60, 120, 365, and 730 days) along the trajectories of larvae successfully crossing the 25°W meridian after release within the *Anguilla anguilla* spawning polygon. The trajectory information has been subdivided according to the 5° latitude bin of arrival at the 25°W meridian. The dotted line gives the average chlorophyll concentration in the polygon defining the spawning region of *A. anguilla*, and the gray shading delimits the minimum and maximum climatological SeaWiFS chlorophyll concentrations within the spawning region. The horizontal bars denote the observed spawning periods for *A. anguilla* (AA) and *Anguilla rostrata* (AR).



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ple, the presence of a preferred 200 m modal migration depth for migration success is consistent with the depth distribution of captures from field studies (Schoth and Tesch 1983; Castonguay and McCleave 1987). It probably originates as a compromise by the organism to avoid slower geostrophic currents deeper in the water column and also avoid southward transport in the North Atlantic storm track region, where the mean westerly winds induce southward transport in the Ekman surface layer. Although the importance of depth selection to the success of the larval migration has not previously been suggested for the European eel larvae, Kimura et al. (1994) suggested that Japanese eel (*Anguilla japonica*) larvae may take advantage of steady, wind-driven surface currents to select the northward bifurcation of the Pacific equatorial currents toward Japan. This, therefore, represents the reverse strategy to the *A. anguilla* migration, which avoids Ekman circulation in the North Atlantic as a migration strategy to reach Europe.

The possibility of a population selection process acting on the basis of spawning location within the Sargasso Sea has been another new concept introduced by this modelling study. Larvae are carried in streams towards Morocco, the Bay of Biscay, and Scotland, and these may correspond to coherent ocean current features (e.g., Gulf Stream, North Atlantic Current, Azores Current) that have been independently identified in drifter studies (e.g., Flatau et al. 2003; Niiler et al. 2003). A closer look at the data reveals that the larvae ending up in different regions of Europe may have chosen different strategies of spawning location and migration depth to use these currents to preferentially target particular regions of Europe and North Africa. The western part of the Sargasso Sea seems to favour a successful transatlantic migration to all latitudes of the adult range in Europe and North Africa. However, the model suggests that there may be a successful transatlantic migration from the northeast corner of the spawning region toward Morocco. In a careful hydrographic study, McCleave (1993) revealed an eastward larval migration route from the eastern part of the Sargasso Sea spawning area, and the results of the present study suggest that this migration may preferentially target Morocco or the Mediterranean.

Eel populations in West Africa?

One unanticipated feature predicted by the model is the apparent larval stream toward equatorial Africa that is carried on the North Equatorial Counter-Current. The larval stream originates within the McCleave et al. (1987) polygon defining the *A. anguilla* spawning area, and there have been two larval captures along its course. The average SeaWiFS ocean colour value along this southern route near the equator is high and may indicate high chlorophyll concentration and food availability. Moreover, the model predictions of the existence of this migration route have been replicated using fields of near-surface geostrophic flow derived from a totally independent set of ocean circulation fields (supplied by R. Lumpkin, Cooperative Institute for Marine and Atmospheric Studies, University of Miami, Rickenbacker Causeway, Miami, FL 33149, USA, personal communication) derived from drogued surface drifters that have been corrected for wind-driven circulation by National Centers for Environmental Prediction (NCEP) winds. Lagrangian drifters originating at the extreme eastern end of the *A. anguilla* spawning zone propagate eastward at the bifurcation point in the Brazil retroflection area. However, in spite of the plausibility of the southern migration route and the availability of shallow brackish lagoons in west Africa, *A. anguilla* has not been recorded south of the Senegal River by fisheries experts in the region (J.J. Albaret, UR RAP (070), IRD, BP 1386, Dakar, Senegal, personal communication) or in archaeological sites in West Africa (W. van Neer, Royal Museum of Central Africa, 3080 Tervuren, Belgium, personal communication). Initial findings of eel landings in Togo (FAO 1983) and Gambia (FAO 1997) have been identified as errors (L. Garibaldi, Fishery Information, Data and Statistics Unit (FIDI), Food and Agriculture Organization of the United Nations (FAO), Viale delle Terme de Caracalla, 00100 Rome, Italy, personal communication) and are not present in the most recent FAO electronic database (http://www.fao.org/fi/statist/statist.asp). Possibly, the shallow migration depth (10–50 m) required by the model to reach equatorial Africa is not consistent with the 200 m migration depth that optimize the success rate of reaching the normal adult range in Europe and North Africa.

On the other hand, this southern route is a viable migration route for some of the North Atlantic eels. It is bounded by the southernmost range of the *A. rostrata* in Guyana and the West Indies (Schmidt 1909), and the model findings resolve a long-standing question of how *A. rostrata* can populate these areas from its spawning zone in the Sargasso Sea against the prevailing surface currents (Meek 1916; Vladykov 1964; Harden Jones 1968). Some North Atlantic eels (although not the European eel), therefore, do take advantage of this southern migration route. From the view of physical oceanography, the Sargasso Sea spawning ranges of *A. anguilla* and *A. rostrata* are located at an important divergence point of North Atlantic circulation. It is interesting to speculate how eel populations and migration routes may have shifted during periods of maximum glaciation to ameliorate habitat loss in northern ice-covered zones and take advantage the tropical refugia in South America and West Africa (e.g., Bradley 1999).

Duration of larval migration

The present model suggests that the duration of the *A. anguilla* larval migration is about 2 years (and less than 1 year for *A. rostrata*). This supports the original conclusions that Schmidt (1923) made on the basis of the propagation of discrete annual cohorts across the Atlantic Ocean. It does not support the much shorter migration period of 1 year or less that was proposed by Lecomte-Finiger (1992) and supported by Desaunay and Guerault (1997) on the basis of the assumed daily deposition of otolith rings. Other findings have suggested that the otolith rings may actually be created at a lesser frequency, and hence the duration of the migration might be considerably longer than early otolith studies have suggested (e.g., Tesch 2003). Interestingly, doubts about the duration of the larval migration had been expressed much earlier by Deelder (1970) on the basis of the shorter time period that it took derelicts to drift across the North Atlantic (e.g., Richardson 1985). On the other hand, using a Lagrangian model based on circulation fields from ship drift statistics, Harden Jones (1968) suggested that the duration of

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the larval migration might last up to 3 years. Schmidt's (1923) initial hypothesis that *A. rostrata* and *A. anguilla* are partitioned on different sides of the Atlantic Ocean on the basis of the duration of their larval life stage (i.e., 1 year for *A. rostrata* and more than 2 years for *A. anguilla*) is consistent with the findings of this modelling study. *Anguilla rostrata* specimens have been identified in northern Europe (Boetius 1980), and hybrids are located in southwest Iceland (Williams et al. 1984) along a fast ocean current that could transport larvae in about 1 year. However, based on ocean currents passing westward from Iceland and on the known distribution of *A. anguilla* on Iceland, Greenland should be populated with *A. anguilla* or hybrids rather than the *A. rostrata* that has been identified (Jensen 1937, Boetius 1985). Likewise, it is unclear why no *A. anguilla* larvae appear in North America after drifting at sea for 2 years. The resolution of these questions may be revealed by careful consideration of the criteria for success required to reach the different North Atlantic locations and the possible effects of larval mortality along the migration routes.

Possible implications for genetic mixing

It was interesting to find out whether the optimum migration strategies required by the model larvae to target particular latitude bins in the eastern Atlantic would also lead to a leakage of larvae into other nontargeted bins. This possibility may be explored using the same concepts of Green's functions and footprint areas that are used in atmospheric chemistry (e.g., Enting 2002) and physical oceanography (e.g., Kettle 2005) to find the relationships between source and receptor regions within an advective–diffusive flow. In this case, the projections shown in Figs. 4 and 5 define tracer source regions that are linked by ocean currents to the receptor latitude bins on the eastern side of the Atlantic Ocean. The source regions and receptor bins are not linked uniquely, and there is an overlap in the migration depths and spawning locations that are required to reach a particular target bin. The relationship between sources and receptors can be represented as a matrix (illustrated in Fig. 9) that shows how the best spawning–migration strategy to reach each latitude bin will also spread larvae to other nontargeted latitude bins. (It must be noted that the numbers of arrivals shown in Fig. 9 will also depend on how the source–footprint regions are weighted and that Fig. 9 was generated on the premise of larval releases spread evenly over all depths, months, and locations in the Sargasso Sea spawning region). Most of the larvae reach the targeted latitude bin, and this suggests that selection for arrival at different regions of Europe or North Africa is quite feasible.

The model forces consideration on how *A. anguilla* can maintain its population structure during the two-way migration across the North Atlantic Ocean. The most recent molecular evidence (e.g., Daemen et al. 2001; Wirth and Bernatchez 2001; Maes and Volckaert 2002) indicates that there is local structure within European eel populations. However, it is unclear whether the molecular characteristics defining the eel subpopulations at a particular location endure through time or they fluctuate temporally over a range that is comparable with spatial variations across the European range (Dannewitz et al. 2005). The former defines a situation where the concept of panmixia may be rejected, and there may actually be mechanisms to prevent gene exchange among the different European subpopulations (Wirth and Bernatchez 2001). If the temporal variation in molecular markers is comparable with the spatial variation, then it becomes ambiguous if special mechanisms are in place to prevent panmictic spawning in the population. There might be a special situation where molecular marker mutations take place at a considerable rate within each generation, and the variations that appear within the Europe populations result from nonrandom transport by ocean currents that may differ from year to year (Williams and Koehn 1984). Summarizing the work of Williams and Koehn (1984), Avise et al. (1986) states " '... it is entirely possible that spawning is essentially panmictic...it means that collections of juveniles from any locality are all samples of the same breeding population'. If it is true that self-maintaining local populations are absent in *Anguilla*, any observed genetically based differences among geographically widespread collections of juveniles '...should represent what natural selection can do in a single generation' ".

It is possible to explore the extent to which the European eel population can be randomized by ocean circulation during a single transatlantic larval migration. Although the model cannot be used to comment on the differential mortality of eels in rivers (Williams and Koehn 1984) or the possibility of assortative mating in the Sargasso Sea, it can be used to test the extent to which tracer structures that are defined in the Sargasso Sea are maintained during a 2-year passive drift. The matrix representation of the Green's functions (Fig. 9) shows how each latitude bin will hold a labelled mixture of larvae from the different footprint regions in the Sargasso Sea. The ratio of the different labelled elements in the mixture varies according to which latitude bin is considered. The mixtures of Green's functions are analogous to mixtures of alleles at a single locus, and chord distances (D_{CE}) among all sets of the 11 populated latitude bins were calculated according to Cavalli-Sforza and Edwards (1967). The distance matrix was used to construct an UPGMA tree (unweighted pair group method with arithmetic mean, shown in Fig. 10*a*; Nei 1987). For comparison, a similar tree (Fig. 10*b*) was constructed from information digitized in Wirth and Bernatchez (2003), which was based on microsatellite analysis of a collection of *A. anguilla* and *A. rostrata* eel samples from 21 locations around the North Atlantic Ocean.

Both the model and experimental UPGMA trees show patterns of relatedness and juxtaposition. For the model (Fig. 10*a*), the tree shows a clear split between the cluster of related latitude bins for Europe and North Africa and the cluster for the (hypothetical) equatorial African populations. Focussing on the group for Europe and North Africa, there is a pattern of clustering of latitude bins starting with the central latitude bins for France and northern Spain–Portugal and successively linking with other latitude bins moving both northward and southward from the central region. There is a general relationship between the model genetic relatedness and latitude distance. One exception to this is the second cluster, where the Morocco latitude bin is linked with the France – northern Spain cluster in preference to the adjacent latitude bin for southern Spain. In this case, the genetic distance is not related to geographic proximity.

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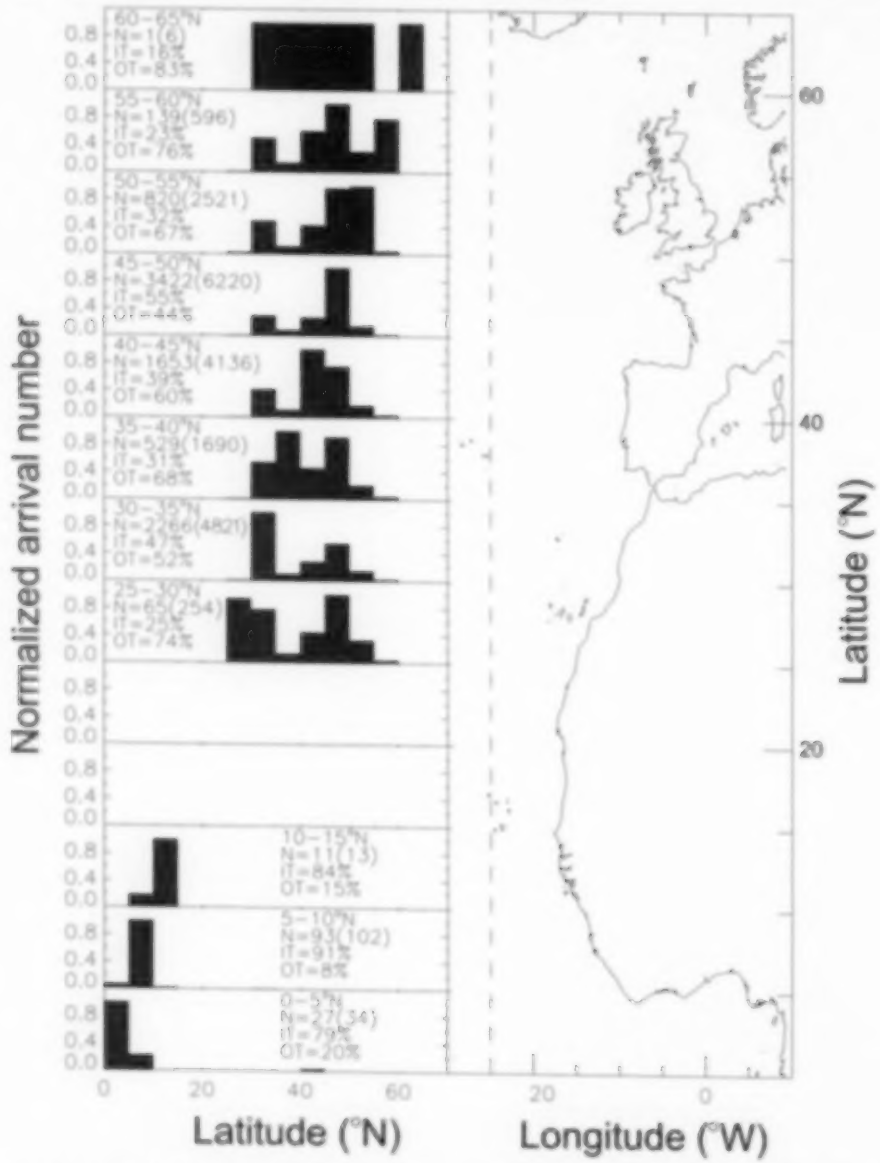
Fig. 9. Spread associated with larvae following a spawning–migration strategy optimized to target a single latitude band. The plots show the other latitude bins where the eel larvae also end up if they pursue a spawning strategy (i.e., location within the *Anguilla anguilla* Sargasso Sea spawning polygon, spawning month, and depth of migration) to reach a particular latitude bin target given by the uppermost text line in each histogram. *N* is the total number of successful eel arrivals in all latitude bins, and IT and OT are the percentages of successful eel arrivals inside and outside their target bin, respectively. The histograms have been normalized by their largest element, which in every case is the number reaching the targeted latitude bin.



The juxtaposition of sample locations is more prominent in the UPGMA tree based on laboratory microsatellite results (Fig. 10*b*). The most important split in this tree is between the *A. rostrata* and *A. anguilla* groups. For the *A. anguilla* group, there is a general pattern of successive clustering based roughly on geographic proximity from a central cluster comprising samples from Germany, France, Norway, and Portugal. Samples from Scandinavia join the central cluster next, followed by samples from southern Europe and the Mediterranean. Examples of juxtaposition of geographic elements are more frequent here, with samples from Norway and Portugal showing a close relationship; samples from Iceland and Atlantic France also show a close relationship. Similar patterns of incomplete juxtaposition were also apparent in the original nearest neighbour trees of Wirth and Bernatchez (2001, 2003) and in the earlier work

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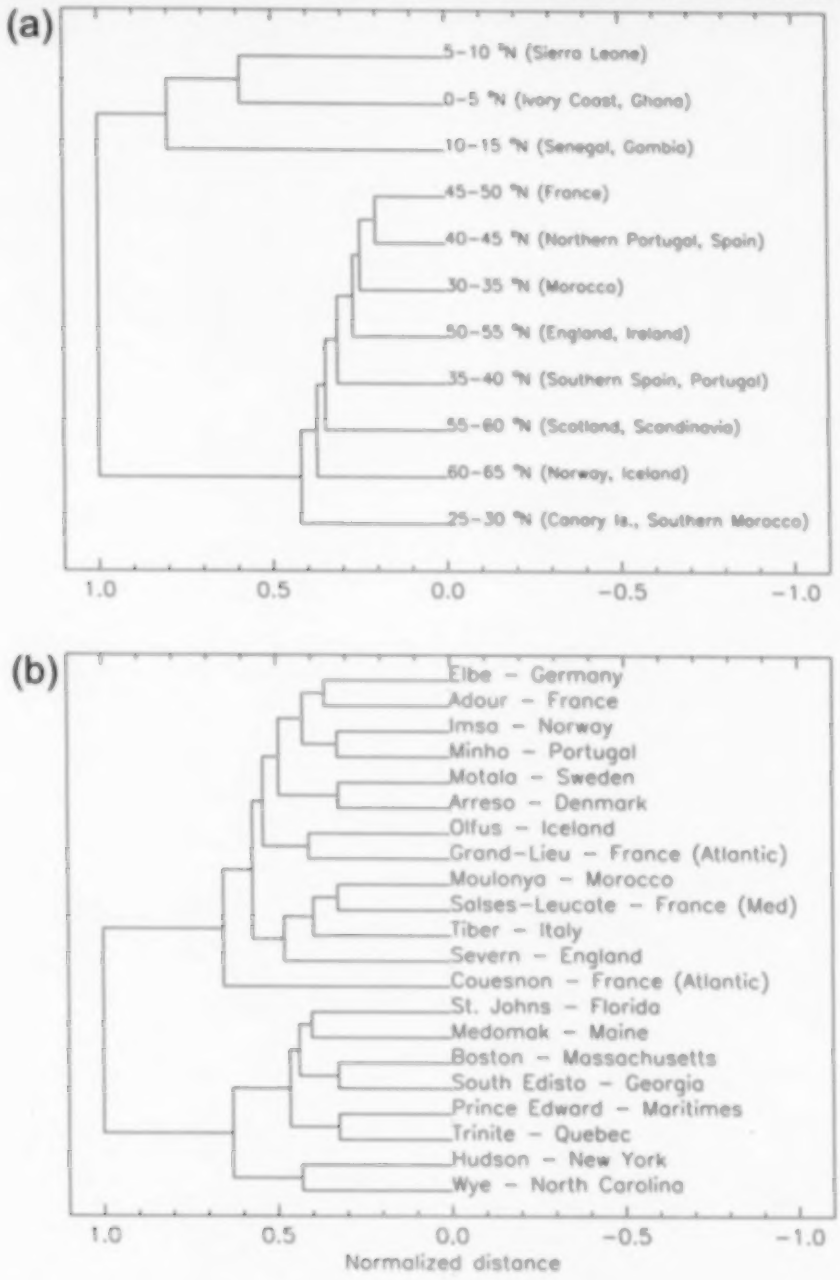
Fig. 10. Unweighted pair group method with arithmetic mean (UPGMA) trees of Cavalli-Sforza and Edwards (1967) genetic distances from the (*a*) Green's function model results shown in Fig. 9 and (*b*) microsatellite results of Wirth and Bernatchez (2003).



of Lintas et al. (1998; as redrawn by Avise 2003). Both the model and the molecular marker studies suggest that a larval population starting in the Sargasso Sea may not be completely randomized during a 2-year passive migration across the North Atlantic Ocean. The nature of the oceanic mixing may be such that the genetic and geographic distance among European eel populations may show signs of juxtaposition.

In describing how to construct UPGMA trees showing the relationships among populations, Nei (1987) pointed out that uncertainties in the genetic distance data could lead to ambi-

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guities in the branching structure of the genetic trees. In the modelling exercise, only two complete migration cycles were available to construct the UPGMA tree in Fig. 10*a*, and it is possible that the consideration of other years for the ocean circulation fields would have led to different tree patterns. This is analogous to possible difficulties in interpreting lab-based molecular marker data, where individuals may show major genetic variation within a larger population or river based on the year of recruitment (Dannewitz et al. 2005).

Future work

In conclusion, this modelling study has served to clarify some long-standing ambiguities and debates surrounding the natural history of the European eel. The release of virtual drifters evenly over all depths, latitudes, and longitudes in the Sargasso Sea spawning region led to their preferentially arriving in certain latitude ranges on the eastern side of the Atlantic Ocean within 2 years. A modal depth of 200 m was favoured for the successful transatlantic migration, consistent with the actual, observed capture depth distribution. Also, drifters had different success rates of reaching the normal adult range based on where they started in the Sargasso Sea spawning zone. These differences could form the basis of a selection strategy that could lead to the retention of population structure in Europe and North Africa during the passive transatlantic migration. The month of spawning is not included in this hypothesized selection procedure because there is no clear relationship between different spawning seasons and successful arrival in different subregions in Europe and North Africa. Rather, it is shown that the spawning time in spring may be part of a general survival strategy to minimize contact with predators in the earliest stages of the migration and maximize phytoplankton (i.e., food) availability during the middle and later stages of the migration.

This study has introduced a number of questions, hypotheses, and projects for further investigation. The most important assertion of the model is that the eel population may not be completely randomized during its passive migration across the North Atlantic Ocean, but that larvae in the Sargasso Sea may be identified with particular eel populations in Europe and North Africa depending on the location, depth, and month of larval capture. There may be a closer association between the larvae of the western Sargasso Sea and the adult eels of northern Europe, and between the larvae of the eastern Sargasso Sea and the eels of southern Europe. This question might be resolved by microsatellite studies (T. Wirth, Department of Biology, Universitaetstrasse 10, University of Konstanz, D-78457, Germany, personal communication) conducted on preserved larval material stored in fisheries laboratories in Denmark, the Netherlands, and the United States, as suggested by McCleave (2003). It is important to realize that the existence of clines in molecular markers within the adult European eel populations might also develop through differential mortality in rivers (Williams and Koehn 1984), and studies of molecular markers as tracers of ocean currents should focus on glass eels just entering rivers.

There are also a number of important issues to be resolved by future modelling investigations. The life cycle of the American eel has been neglected in this modelling study, and it would form an interesting investigation by itself. Using microsatellites, Wirth and Bernatchez (2003) identify no population structure in *A. rostrata*, and it is unclear if a modelling study could reproduce this result. A combined modelling study of *A. anguilla* and *A. rostrata* might also investigate the hybrid status of the Iceland eels (Williams et al. 1984, Avise 2003). The influence of larval mortality could form the basis of another modelling investigation. Possibly, the transatlantic larval migration would not be successful if the mortality rate was as high as that assumed by Cowen et al. (2000), but the relationship among the number of spawners, female fecundity, and larval mortality is not clear for the European eel. Uncovering the reason for the vertical, diurnal migration of the larvae could form another investigation. Field studies have established that the larvae from an early stage of development show evidence of vertical, diurnal migrations and come near the sea surface at night (Schoth and Tesch 1983; Castonguay and McCleave 1987). In addition to possible advantages of securing food and avoiding predators, this vertical migration strategy may provide the larvae with an additional means of taking advantage of currents at different depths and targeting particular adult range locations in Europe and North Africa. Finally, numerical investigations could be used to explore how depletions of localized European eel populations (i.e., through overfishing or disease) may impact stocks in more distant regions, an economic issue that was first raised by Petersen (1905; see also Harden Jones 1968).

To some extent, the data-assimilated circulation fields chosen for the present investigation may not have been optimal for investigating the migration strategy of the European eel. There was only 4 years of circulation information to investigate the characteristics of a 2-year migration period, and it spanned a switch in phase of the North Atlantic Oscillation (NAO; the pressure difference between Iceland and Portugal). The NAO is associated with significant changes in wind circulation and has an important impact on ocean circulation (Flatau et al. 2003). The fluctuations in the NAO may lead to perturbations in the eel larvae recruitment success (Knights 2003). However, the 4-year period covered by the fields was not long enough to allow a systematic study of the larval recruitment success associated with interannual changes in North Atlantic circulation. With long-term fields from a number of data-assimilated ocean circulation projects becoming available (e.g., the 40-year oceanographic reanalysis project ENACT (ENhAnced ocean data assimilation and ClimaTe prediction), which is archived at http://www.nerc-essc.ac.uk/godiva), future investigations might explore if interannual changes in ocean circulation have an effect in the randomization of the gene pool of the European freshwater eel. Ultimately, the new ocean circulation fields may be used to help probe the causes of the drastic decline in eel numbers over the past 20 years.

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Amsterdam (Mr. Jip Binsberger and Ms. Joke Bleeker) helped to obtain older, difficult sources. Records of larval captures outside of the available literature have been provided by Prof. D. Schnack (Institut für Meereskunde, Kiel), Dr. B. Strehlow, and Dr. F.-W. Tesch. We appreciate the detailed comments of Dr. B. Knights and one anonymous reviewer in helping us to improve the manuscript.

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Fine-scale geographic interactions between Steller sea lion (*Eumetopias jubatus*) trends and local fisheries

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Abstract: Fine-scale geographic interactions between Steller sea lion (*Eumetopias jubatus*) abundance trends and the abundance of local fisheries and commercial fishing efforts from Southeast Alaska to the Aleutian Islands were assessed. Census counts of Steller sea lions from 1976 to 2002 at 53 different trend sites and rookeries were grouped into 33 locales with similar population trends. Localized estimates of commercial groundfish biomass densities for walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*), and Atka mackerel (*Pleurogrammus monopterygius*) from 1983 to 2002 and localized estimates of commercial fishing effort from 1990 to 2002 were matched to the 33 locales. Generalized estimating equations methods found a negative relationship between Steller sea lion abundance trends and walleye pollock density ($P < 0.10$). However, the 4.8-fold change in walleye pollock density between 1984 and 2001 was estimated to change the rate of population change (λ) by only 0.029. The analysis estimated that elimination of all trawl fishing effort would increase λ by as little as 0.0056. Neither commercial groundfish abundance nor commercial fishing effort could explain the large historical declines in the rate of Steller sea lion population change observed.

Résumé : Nous avons évalué les interactions sur une échelle géographique fine entre les tendances de l'abondance des lions de mer de Steller (*Eumetopias jubatus*), d'une part, et l'importance des pêches locales et des efforts de pêche commerciale du sud-est de l'Alaska jusqu'aux îles Aléoutiennes, d'autre part. Nous avons regroupé les données des recensements de lions de mer de Steller de 1976 à 2002 à 53 différents sites d'inventaires et roqueries en 33 ensembles spatiaux présentant des tendances démographiques semblables. Nous avons ensuite associé ces 33 ensembles à des estimations en des points précis de la densité de biomasse de poissons de fond commerciaux, la goberge d'Alaska (*Theragra chalcogramma*), la morue du Pacifique (*Gadus macrocephalus*), la plie à grande bouche (*Atheresthes stomias*) et le maquereau d'Atka (*Pleurogrammus monopterygius*) de 1983 à 2002, ainsi qu'à des estimations à des points précis de l'effort de pêche commerciale de 1990 à 2002. L'utilisation d'équations d'estimation généralisées révèle une relation négative entre les tendances d'abondance des lions de mer de Steller et la densité des goberges de l'Alaska ($P < 0,10$). Nous avons estimé, cependant, que la variation de densité de la goberge de l'Alaska par un facteur de 4,8 entre 1984 et 2001 n'a modifié le taux de changement de la population (λ) que de 0,029. L'analyse montre que l'élimination de tout effort de pêche au chalut augmenterait λ par aussi peu que 0,0056. Ni l'abondance des poissons de fond d'intérêt commercial, ni l'effort de pêche commerciale ne permettent d'expliquer les importants déclins dans le taux de changement de la population de lions de mer de Steller observés dans le passé.

[Traduit par la Rédaction]

Introduction

The long history of human – marine mammal interactions has been a history of often severe negative impacts. Intensive direct harvest into the 20th century severely depleted populations across the globe (Doroff et al. 2003; Roman and Palumbi 2003; Hucke-Gaete et al. 2004). Commercial exploitation nevertheless is not the only source of fisheries impacts. Marine mammal populations have also suffered through direct interactions with commercial fishing. Bycatch of marine mammals occurs in net fisheries (Read and Wade 2000), and individual populations may be threatened by this incidental take (Dans et al. 2003). However, competition for fish stocks between commercial fisheries and marine mammals may be the primary source of current and future conflicts (Trites et al. 1997; DeMaster et al. 2001). In the North Atlantic Ocean, Kaschner et al. (2001) observed that among all marine mammal species studied, foraging pinnipeds

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along the continental shelf had the most overlap with commercial fisheries. Another example of possible competition occurs in the North Pacific, where Steller sea lions (*Eumetopias jubatus*) have undergone a precipitous decline (Braham et al. 1980; Merrick et al. 1987; Loughlin et al. 1992). Steller sea lion populations declined by as much as 60% range-wide between the early 1950s and a comprehensive survey in 1989 (Loughlin et al. 1992). The continued decline of the United States population from Prince William Sound westward led to classification under the Endangered Species Act in the United States in 1997 (Rosen and Trites 2000).

The Steller sea lion population is divided into two distinct subpopulations, defined spatially into eastern and western stocks (Bickham et al. 1996; York et al. 1996; Loughlin 1997), and differing widely in their abundance trends and classification under the Endangered Species Act in the United States. The population of the western stock has declined precipitously since the 1950s (Merrick et al. 1987; Loughlin et al. 1992; Rosen and Trites 2000), while the eastern portion of the stock remains healthy (Calkins et al. 1999). Reasons for the decline are unknown, but the widespread decline seen in Steller sea lion populations in the Gulf of Alaska and the Aleutian Islands suggests large-scale factors may be at work. However, there has also been considerable spatial variation in the timing and scale of decline (York et al. 1996), suggesting that there are subregional and localized effects at work as well.

Steller sea lions feed on a wide variety of prey, and their diet reflects seasonal and spatial variations in the availability of prey (Pitcher 1981; Calkins and Goodwin 1988; Sinclair and Zeppelin 2002). The Bering Sea ecosystem has shifted since the 1950s, with a major regime shift in 1976–1977 (Francis et al. 1998; Barange 2003; Beamish et al. 2004). Formerly dominated by crab, shrimp, and pelagic fishes, it became dominated by walleye pollock (*Theragra chalcogramma*) and flatfish (Trites et al. 1999; Barange 2003). However, because gadids such as walleye pollock are not as fatty as small forage fish and are harder to digest, they may not provide adequate nutrition (Rosen and Trites 2000; Trites and Donnelly 2003). Alternatively, a lack of diet diversity (Merrick et al. 1997) or inadequate density of forage fish including walleye pollock (Sinclair and Zeppelin 2002; Winship and Trites 2003) may be to blame.

Inadequate prey quality has been one of the hypothesized causes of nutritional stress in Steller sea lion (Rosen and Trites 2000; Trites and Donnelly 2003). Diet experiments (Rosen and Trites 2000) support the hypothesis that a heavy reliance on walleye pollock may have an adverse effect on the overall health of sea lions. High walleye pollock or Pacific cod (*Gadus macrocephalus*) densities could have a negative effect on the availability of high-fat content fish such as Pacific herring (*Clupea pallasii*) and capelin (*Mallotus villosus*), thus decreasing both prey diversity and density. Consequently, an ecosystem dominated by walleye pollock at the expense of other species may have a negative effect on sea lions. Additionally, walleye pollock are cannibalistic, so high densities of adult walleye pollock may reduce levels of juvenile walleye pollock favored by sea lions, especially juvenile sea lions (Alverson 1992; Merrick and Calkins 1996).

Commercial fishing activity has also been considered a factor in Steller sea lion declines (Alverson 1992), whether because of disruptions of foraging behavior (Fritz and Ferrero 1998), bycatch, shooting by fisherman (Alverson 1992), disruption of forage fish aggregations (Sinclair and Zeppelin 2002), or by depletion of local fish stocks (Fritz and Ferrero 1998; DeMaster et al. 2001). Of these, depletion of local fish stocks is most likely to cause a major impact (DeMaster et al. 2001). Additionally, intensive fishing may lead to decreased diversity of fish stocks (Barange 2003), one of the hypothesized causes of sea lion decline (Merrick et al. 1997). Past studies (Loughlin and Merrick 1988; Ferrero and Fritz 1994) have examined relationships between sea lions and walleye pollock catch, with equivocal results.

This study seeks to determine whether localized changes in Steller sea lion distribution and abundance are related to the availability of fish stocks and (or) the level of commercial fishing effort. To do this, a fine-scale geographic analysis that incorporates both temporal and spatial information was developed. Historical data sets on Steller sea lion abundance, commercial groundfish density, and commercial fishing effort were combined for the analysis. The relationship between Steller sea lion population trends and the biomass density of four commercial groundfish species common in sea lion diet (walleye pollock, Pacific cod, arrowtooth flounder (*Atheresthes stomias*), and Atka mackerel (*Pleurogrammus monopterygius*)) was examined. Additionally, the relationship between Steller sea lion abundance trends and the amount of time commercial fishing boats were in proximity to haulout sites (nonbreeding locations) and rookeries (breeding areas) was assessed. This approach expands on earlier studies (Loughlin and Merrick 1988; Ferrero and Fritz 1994; Merrick et al. 1997) by adding a fine-scale spatial dimension. Thus, we were able to examine two of the proposed causes of sea lion decline on a fine-scale level, but across a broad geographic range. Hucke-Gaete et al. (2004) provided an example of fine-scaled analysis of population trends on Antarctic fur seal (*Artocephalus gazella*) rookeries in the South Shetland archipelago. A fine-scale analysis approach may be applicable to other populations undergoing rapid population change across a broad range, such as sea otters (*Enhydra lutris*) in the Aleutian archipelago (Doroff et al. 2003). Additionally, ecosystem-based management systems are in need of further development (Barange 2003), and this approach may help quantify the predator–prey–fisheries interactions.

Materials and methods

Historical data

Three primary sources of historical data were used in this investigation. The following sections describe the compilation and characterization of the Steller sea lion census counts, commercial fish densities, and fishing effort used in subsequent regression analyses.

Sea lion abundance and trends

The National Marine Mammal Laboratory (NMML) of the National Marine Fisheries Service (NMFS) of the US Department of Commerce provided historic Steller sea lion

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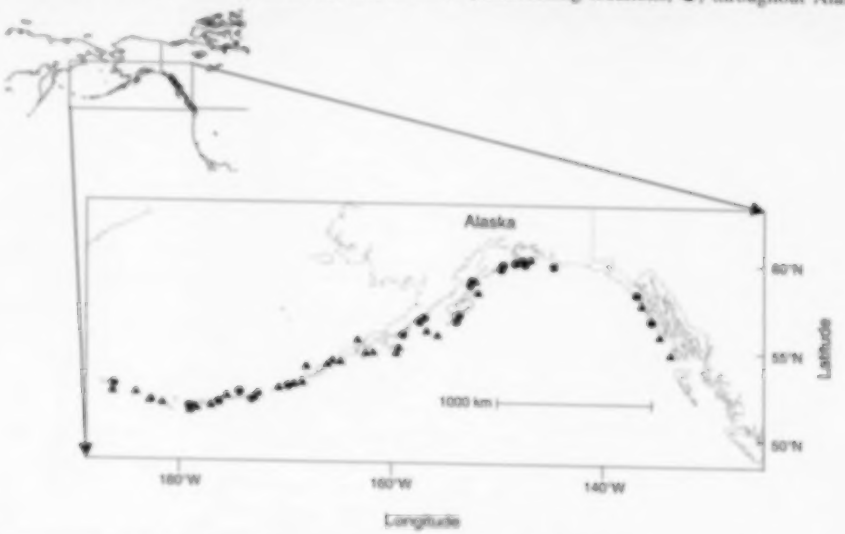
Fig. 1. Locations of 53 trend rookeries (breeding areas; ▲) and haulouts (nonbreeding locations; ●) throughout Alaska, USA.



counts collected by them and other agencies and scientists from 1976 to 2002. Sea lion counts were recorded at both rookeries and haulouts. Following a range-wide survey in 1989 (Loughlin et al. 1992), frequent surveys of adults (non-pups) at select "trend" rookeries and haulouts have been conducted approximately every 2 years. Adults are typically counted via aerial surveys from mid-June to early July, the peak of the breeding season (Calkins and Pitcher 1982). In addition to site-specific data, census locations in the database are grouped into seven larger regions: Southeast Alaska; Eastern, Central, and Western Gulf of Alaska; and Eastern, Central, and Western Aleutian Islands. Southeast Alaska is part of the threatened eastern stock, which stretches from 144°W south to California, while the other locations are part of the endangered western stock, which extends to northern Japan. In addition to differing population trends defining the split (Loughlin 1997), there are genetic differences as measured by mitochondrial DNA between the two stocks (Bickham et al. 1996). Continuously occupied census locations that are part of the trend locations used in NMML population surveys and that had at least 100 Steller sea lions present during the 1989 range-wide survey were included in this analysis. We chose to limit locations by size, because the coefficient of variation is smaller for census locations with larger counts, and we chose 1989 as our benchmark year because it was the beginning of the range-wide surveys (Loughlin et al. 1992). In some cases, multiple counts at a given location were available in a particular year; in these cases, the median of the counts was used. Ultimately, 53 rookeries and haulouts were included in the analysis: 5 from Southeast Alaska, 22 from the Gulf of Alaska, and 26 from the Aleutian Islands (Fig. 1).

In many years, a small number of census locations would be missed by the survey. Missing census locations were generally attributable to poor weather or equipment problems. For analysis purposes, missing census values were problematic. Hence, a missing-values algorithm for a two-way analysis of variance (ANOVA) (Zar 1984) was used to estimate counts. This algorithm treated years and census locations as design factors and used the natural log of the census counts in the algorithm rather than the actual counts. Estimated counts came from back-transforming estimated log counts. A log-linear model was used to estimate the missing values because it was felt the effect of year and location would have a multiplicative effect on abundance. The smallest geographic scale available was used in the missing values algorithm. Ultimately, there were $N = 604$ counts used in the analysis, of which 555 (92%) were actual counts and 49 (8%) were estimated counts.

We observed that the rate of population change varied over the course of time at many census locations. Typically, there were two distinct rates of change observed. For example, census locations in the Central Aleutian Islands generally exhibited a steep rate of decline followed by a more gentle decline or gradual recovery. Thus, we estimated an initial rate of population change (r_1), a secondary rate of population change (r_2), and the year (spline year) the rate of population change shifted. Consequently, we chose spline regressions to model Steller sea lion counts at the ith site in the nth year ($P_{i,n}$) as follows:

$$(1)\qquad \ln(P_{i,n}) = \ln(P^{\text{est}}_{i,\text{spline year}_i}) + r_{i,1}\min[0, n - \text{spline year}_i] + r_{i,2}\max[0, n - \text{spline year}_i]$$

where spline year$_i$ could take integer values from the second to the second-to-last survey year. Maximum likelihood estimation was used to estimate parameters. The intercept parameter $P^{\text{est}}_{i,\text{spline year}_i}$ is interpreted as the natural log of the estimated count at the spline year; the first regression coefficient $r_{i,1}$ is the instantaneous annual rate of population change prior to the spline year; and $r_{i,2}$ is the instantaneous annual rate of change after the spline year.

In census locations where a nested F test indicated that $\Pr(r_1 = r_2) > 0.10$ (e.g., a simpler model would work as effectively as eq. 1, we concluded that there was no substan-

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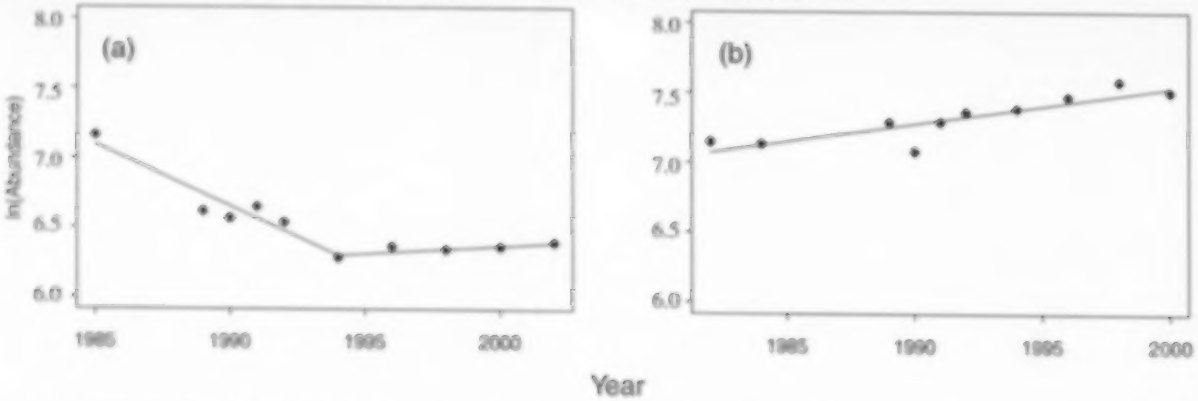
Fig. 2. Population trends and fitted spline regression lines at (*a*) Gramp Rock and (*b*) Hazy Island.



tive difference in rates of population change over time and modeled the data as follows:

$$(2) \qquad \ln(P_{t,n}) = \ln(P^{\text{est}}_{t,1980}) + r_t(n - 1980)$$

For example, at the Gramp Rock rookery in the Central Aleutian Islands, the population declined from 1290 Steller sea lions in 1985 to 537 animals in 1994, followed by a gentle rise to 600 animals in 2002 (Fig. 2*a*). From this, we estimated a rate of decline from 1985 to 1994 ($\hat{r}_1 = -0.088$; standard error (SE) = 0.010) and a rate of increase from 1994 to 2002 ($\hat{r}_2 = 0.011$; SE = 0.010). At Hazy Island in Southeast Alaska, the Steller sea lion census count has climbed gradually from 1268 animals in 1982 to 1824 sea lions in 2000 (Fig. 2*b*). When fitting the best spline regression for Hazy Island, we calculated that $\Pr(r_1 = r_2) = 0.17$, so we concluded that the simpler model would suffice and estimated a single rate of population change ($\hat{r} = 0.026$; SE = 0.005) for the entire period from 1982 through 2000. For most census locations (47 of 53), a spline regression was the preferred model.

Many census locations close to each other were observed to follow similar population patterns over time. In the interest of spatial correlation and data reduction, spatially close census locations that followed the same patterns of decline or growth were grouped together while maintaining as fine a scale as possible. Consequently, after the spline analysis, we performed a cluster analysis using distance, the spline year, and the two spline slopes as input variables. The agglomerative clustering technique (Everitt 1993) was used, based on Euclidean distance and the group average method. Between one and four neighboring locations of the 53 census sites were grouped together, forming 33 clusters. The clusters selected by the algorithm conformed well to a visual estimation of the appropriate clusters. For example, among seven sites in the Andreanof Islands, all sites were characterized by initial steep rates of decline. However, in the eastern Andreanof Islands, the declines changed to modest rates of increase over time, while sites in the western Andreanof Islands generally continued to exhibit modest declines. Thus, three sites in the eastern Andreanof Islands were grouped into one cluster, and four sites in the western Andreanof Islands were grouped into another (Fig. 3).

After the census locations were assigned to clusters, the counts at all locations within each cluster were summed annually, and the spline regression technique previously described was repeated on the pooled data. For each cluster and year, an estimated instantaneous rate of population change ($\hat{r}$) and the associated variance estimate for the predicted rate of population change ($\widehat{\text{Var}}(\hat{r})$) were calculated. While analyses are conducted on r, we will generally discuss the annual rate of population change (λ) or the fractional increase or decrease in annual rate of change ($\lambda - 1$) for ease of interpretation. The instantaneous annual rate of population change (r) is related to the annual rate of population change (λ) by the equation $\lambda = e^r$.

Commercial fish densities

The Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center (AFSC) at NMFS provided bottom trawl survey data from 1983 to 2002 used to estimate groundfish biomass density for walleye pollock, Pacific cod, arrowtooth flounder, and Atka mackerel. The 1983 and 1986 Aleutian Island surveys were conducted cooperatively with the Japan Fishery Agency and employed multiple gear types and towing speeds, which added more variability than subsequent surveys (Ronholt et al. 1994). Bottom trawl survey data from RACE provided estimates of groundfish density near the 33 clusters of Steller sea lion haulouts and rookeries throughout Alaska, typically every 3 years. The bottom trawl survey employs a sampling method stratified by water depth, bottom type, geographic area, and other aspects (Britt and Martin 2001). The survey data provided information on four species of groundfish common in Steller sea lion diet (Pitcher 1981; Sinclair and Zeppelin 2002) and used in this analysis: walleye pollock, Pacific cod, Atka mackerel, and arrowtooth flounder.

For each year of survey data, all trawls within a 74 km (40 nautical mile) radius of a Steller sea lion cluster center (centroid) were identified (Fig. 4). Density of fish, measured as biomass per area (kg·km^{-2}) was calculated from the survey data by summing the biomass caught and dividing by the total area swept by the identified trawls. Only tows longer than 7.5 min in duration were used in the analysis. The biomass estimates provide a local index of the density of fish living in the near zone of a Steller sea lion cluster. Owing to survey

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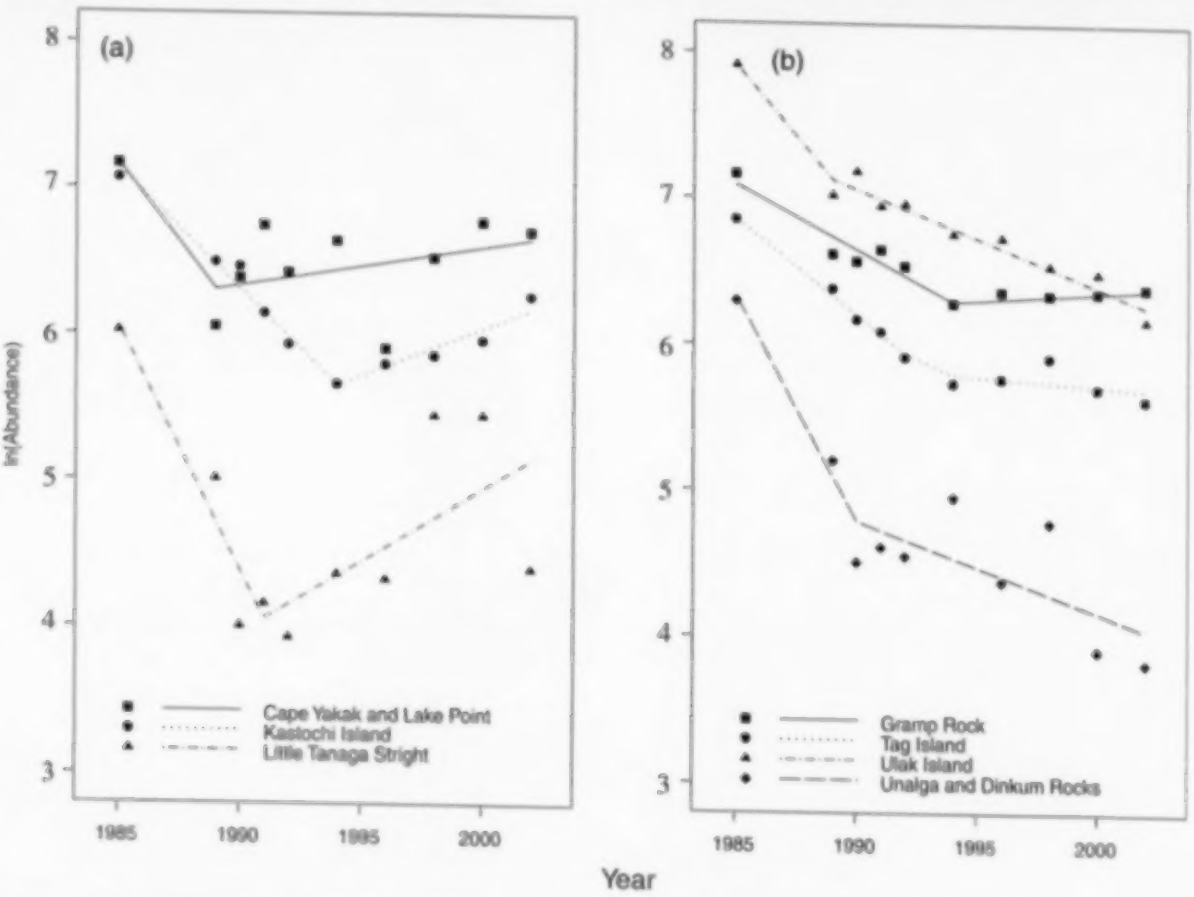
Fig. 3. Population trends and fitted spline regressions for (*a*) the eastern Andreanof Islands cluster and (*b*) the western Andreanof Islands cluster.



limitations based on terrain, size selectivity, fish vulnerability, and other factors, these estimates should be considered indices of abundance rather than absolute abundance (Britt and Martin 2001). The 74 km radius was determined as the smallest area that provided enough information for density estimation at all census locations and is consistent with foraging behavior estimated by radio and satellite-linked telemetry data for 10 adult females (Merrick and Loughlin 1997). Additionally, we calculated fish densities to a radius of 185 km for use in sensitivity analyses.

Commercial fishing effort

The Resource Ecology and Fisheries Management Division of AFSC provided commercial fishing effort data for trawl and longline vessels greater than 18.3 m in length through the North Pacific Groundfish Observer Program (NPGOP). Data from NPGOP was available beginning in 1990. The observer program is administered by AFSC but is implemented by for-profit, private companies. NPGOP places trained observers on commercial fishing boats to monitor levels and composition of commercial catch, along with other goals. The level of coverage varies depending on boat length and gear type, as well as by other regulations. Trawl and longline vessels greater than 38.1 m in length are required to have observers on board 100% of the time. Vessels between 18.3 and 38.1 m in length must have observers on board at least 30% of the time, and vessels under 18.3 m are not required to have observers on board. Vessels in the 30% coverage category can, to some extent, select when observers may be on board (MRAG Americas, Inc. 2000). Furthermore, the lack of coverage in vessels under 18.3 m in length limits the program's ability to monitor fishing catch and effort throughout the entire fleet. While the NPGOP data has limitations, it provides a historical record of commercial fishing trends from 1990 to the present for a select class of fishing vessels.

For each year from 1990 to 2002, we selected all hauls within a 74 km radius of each Steller sea lion census location (haulout, rookery, or grouped cluster), similar to the treatment of the bottom trawl data. The total yearly duration of fishing effort (in days), as well as the biomass caught (metric tons), for each census location were calculated by summing effort and catch data from the selected hauls. For example, 100 days of effort might represent 25 boats fishing for 4 days or four boats fishing for 25 days. Effort and catch data were stratified by vessel length (18.3–38.1 m, >38.1 m)

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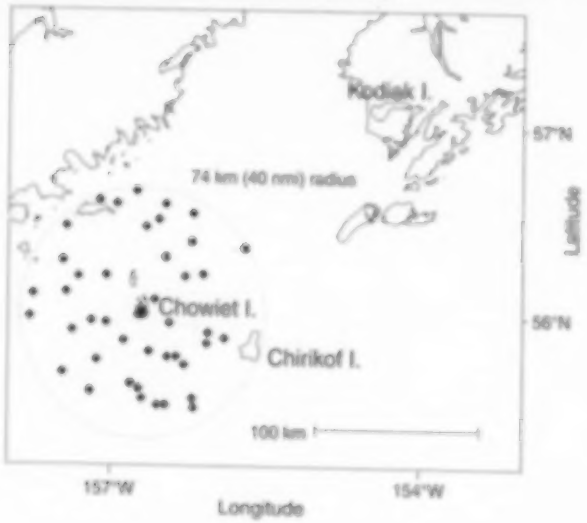
Fig. 4. Example of a cluster center and all trawls (◆) within a 74 km radius of the Chowiet Island rookery.



and gear type (trawl, longline). For clusters of multiple Steller sea lion census locations, the centroid of the census locations was used as the center for the 74 km radius. Catch and effort for vessels in the 30% coverage category were multiplied by 3.33 to make them as comparable with the 100% coverage vessels as possible. This method provided an approximate index of catch and effort. Locations with a higher proportion of 30% coverage vessels would produce estimates with greater sampling variance than locations with primarily 100% coverage vessels.

There are various transit and trawl restrictions around most rookeries and haulouts. Restrictions vary by location and have changed over time, but typically include a 5.6 km no transit zone and 18.5 or 37.0 km trawl restriction zones, some of which are seasonal in nature (NMFS 2001). Restrictions generally increase from east to west (NMFS 2001). Thus, allowed fishing effort is not uniform throughout the 74 km range. In particular, effort generally takes the shape of an annulus (or donut shape), with an outer radius of 74 km and an inner radius that varies by gear type, location, and year, but is generally 5.6 km for longline vessels and 5.6, 18.5, or 37.0 km for trawl vessels, with seasonal variation possible (Figs. 5*a*, 5*b*). In particular, longline vessels are typically allowed to fish closer to rookeries and haulouts than trawl vessels are allowed. Dillingham et al. (2004) provides a complete set of data tables used in this analysis and further descriptions of the raw data.

Statistical methods

We were interested in assessing whether a relationship exists between Steller sea lion abundance trends and commercial groundfish density and (or) commercial fishing effort. For each Steller sea lion census cluster, we assumed a relationship of the form

$$(3) \qquad N_{ijk} = N_{i,j-1,k}\, e^{g(R,Y,X)}$$

where Steller sea lion abundance at the ith location in the jth year in the kth region is a function of the previous year abundance and the possible effects of region (R), year (Y), and other measured covariates (X). Dividing both sides of eq. 3 by $N_{i,j-1,k}$ yields

$$(4) \qquad \frac{N_{ijk}}{N_{i,j-1,k}} = \lambda_{ijk} = e^{g(R,Y,X)}$$

Log transforming both sides of eq. (4) yields

$$(5) \qquad \ln \lambda_{ijk} = r_{ijk} = g(R,Y,X)$$

where the instantaneous annual rate of sea lion population change (r) is modeled as a function of design variables and measured covariates.

Three models were used to test the relationship between estimated Steller sea lion population trends and commercial groundfish abundance. For each of the four species of commercial groundfish studied, the first model is expressed as

$$(6) \qquad \hat{r}_{ijk} = \beta_0 + \beta_{fish} \ln(\text{fish}_{ijk})$$

where $\hat{r}_{ijk}$ is the estimated instantaneous annual rate of sea lion population change for the jth observation in the ith cluster in the kth region (Southeast Alaska, Gulf of Alaska, Aleutian Islands), β_0 is the intercept, β_{fish} is the slope of the regression line, interpreted as the change in $\hat{r}_{ijk}$ for each unit change in $\ln(\text{fish}_{ijk})$, and fish_{ijk} is fish density (kg·km^{-2}) for the ith cluster in the jth year in the kth region. This equation and those that follow were used to test our null hypothesis of no relationship between $\hat{r}$ and ln(fish). In exploratory analysis, the natural logarithm of fish density had superior predictive power (i.e., R^2) than untransformed fish density, so it was used as the fish density covariate in all models. Additionally, we examined quadratic relationships between $\hat{r}$ and ln(fish), but found no significant quadratic relationships for any of the four species studied ($P > 0.10$).

The second model adjusts for broad regional effects via region-specific intercepts and can be expressed as follows:

$$(7) \qquad \hat{r}_{ijk} = \beta_{0,k} + \beta_{fish} \ln(\text{fish}_{ijk})$$

where $\beta_{0,k}$ is the region-specific intercept used to test for differences across regions. Additionally, we examined region by fish interaction effects, but found none that were significant ($P > 0.10$).

The third model adjusts for both regional and temporal effects that vary by region, as follows:

$$(8) \qquad \hat{r}_{ijk} = \beta_{0,k} + \beta_{year,k}\, \text{year}_j + \beta_{fish} \ln(\text{fish}_{ijk})$$

where year_j is the jth year, treated as a continuous variable, and $\beta_{year,k}$ is the yearly change in $\hat{r}_{ijk}$ within the kth region.

We included region and year effects for several reasons. While main effects models such as that described by eq. 6 describe broadscale relationships, much of the variability in both Steller sea lion abundances and fish densities can be explained by regional and year-to-year differences. Thus, any association between $\hat{r}$ and ln(fish) seen in eq. 6 is confounded with time and space. Variability in Steller sea lion abundance trends not explained by time and space could be accounted for by local variations in fish density. Hence, statistically significant relationships between fish density and sea lion abundance, after adjusting for time and space,

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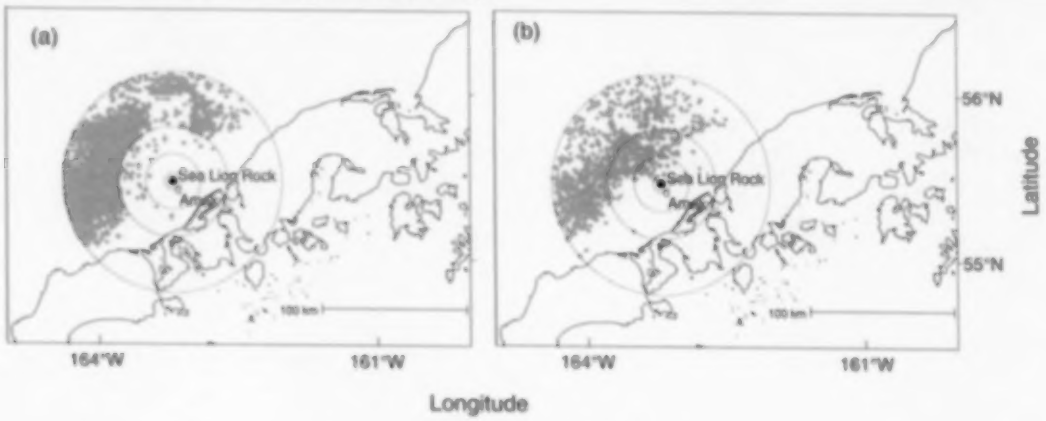
Fig. 5. Locations of (*a*) commercial trawl and (*b*) commercial longline fishing effort within 74 km of Sea Lion Rock near Amak Island in 2000. Circles centered on Sea Lion Rock with radii of 5.6 m, 18.5 m, and 37.0 km correspond to the outer limits of no transit, no trawl fishing, and no winter trawl fishing zones, respectively.



would strengthen the evidence for the association. Additionally, multispecies groundfish models were analyzed. However, additional data on biomass density of other prey fishes such as salmon, herring, and eulachon would be necessary to develop a truly satisfactory multispecies model. Our analyses were limited to single species and multispecies groundfish extensions of models 6–8.

To assess the relationship between Steller sea lion abundance trends and trawl or longline fishing effort, three similar regression models were developed:

$$(9)\quad \hat{r}_{ijk} = \beta_0 + \beta_{trawl}\,\text{trawl}_{ijk} + \beta_{longline}\,\text{longline}_{ijk}$$

$$(10)\quad \hat{r}_{ijk} = \beta_{0,k} + \beta_{trawl}\,\text{trawl}_{ijk} + \beta_{longline}\,\text{longline}_{ijk}$$

$$(11)\quad \hat{r}_{ijk} = \beta_{0,k} + \beta_{year,k}\,\text{year}_j + \beta_{trawl}\,\text{trawl}_{ijk} + \beta_{longline}\,\text{longline}_{ijk}$$

where trawl_{ijk} is the number of days of trawl fishing effort for vessels >18.3 m for the ith cluster in the jth year in the kth region, and longline_{ijk} is the number of days of longline fishing effort for vessels >18.3 m for the ith cluster in the jth year kth region. Additionally, because fishing effort was substantially different in scale and makeup and had different fishing regulations in Southeast Alaska, we performed all analyses with and without Southeast Alaska locations included. Two locations (Sea Lion Rock near Amak Island and the Akutan Island vicinity) had substantially higher levels of fishing effort than other locations. Models were also run with and without these two locations included.

We wish to interpret the effect that a change in a covariate x with corresponding coefficient β_x has on annual rates of Steller sea lion population change (λ). For example, if x changes to $x + \Delta x$, the corresponding changes of r to $r + \Delta r$ and λ to $\lambda + \Delta\lambda$ can be calculated. First, note that for all regression models (eqs. 6–11)

$$\Delta r = \beta_x \Delta x$$

$$\text{Using } \Delta r = \ln(\lambda + \Delta\lambda) - \ln\lambda = \ln\left(\frac{\lambda + \Delta\lambda}{\lambda}\right), \text{ then}$$

$$\Delta\lambda = [\exp(\beta_x \Delta x) - 1]\lambda$$

or equivalently

$$(12)\quad \frac{\Delta\lambda}{\lambda} = \exp(\beta_x \Delta x) - 1$$

where $\Delta\lambda/\lambda$ is the fractional change in λ for a change of Δx in the independent variable. For example, if $\beta_x = -0.008$, then the estimated change in λ from a 10 unit increase in x is $\widehat{\Delta\lambda/\lambda} = \exp(-0.008 \times 10) - 1 = -0.077$, or a 7.7% decline in the annual rate of Steller sea lion population change (i.e., λ would decrease to $(1 - 0.077\lambda)$). In the case where $\lambda = 1$, eq. 12 expresses the absolute change in λ for a change in Δx in the independent variable.

We used weighted regression with weights proportional to $1/\widehat{\text{Var}}(\hat{r}_{ijk})$ for all analyses. All regression models were fit using generalized estimating equation (GEE) algorithms (PROC GENMOD, SAS Institute Inc., Cary, North Carolina; Diggle et al. 1994). The GEE approach incorporates the within-site temporal correlation, thus giving more accurate estimates of the SEs of model parameters and is generally more conservative than a general linear model (GLM) approach. Normal errors and an exchangeable correlation structure were used for all models. A Z test was used to determine significance of the regression coefficients. All significance tests were conducted at the $\alpha = 0.10$ level.

Results

Steller sea lion trends

Overall, the populations of Steller sea lions at our Alaskan locations, estimated at over 100 000 animals in the late 1970s, declined to only 25 000 by the end of the millennium. The population loss in Alaska was a result of declines in the western stock of Steller sea lions from 144°W westward through the Aleutian Islands. Steep rates of decline were seen across the Gulf of Alaska and the Aleutian Islands in 1985, when the mean annual rates of decline were 15.0% and 17.1%, respectively. Population trends moderated or stabilized by 2000 in many locations (Fig. 6) to mean annual declines of 3.1% in the Gulf of Alaska and 4.4% in the Aleutian Islands. Steller sea lions in Southeast Alaska, part

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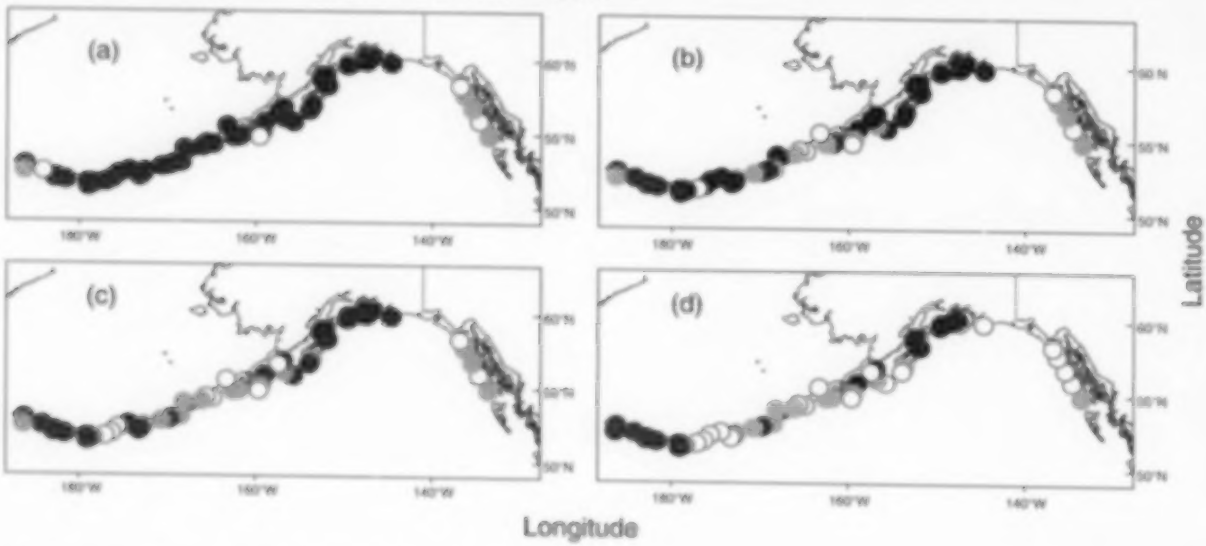
Fig. 6. Annual rates of population change (>6% decline, solid circles; 0%–6% decline, shaded circles; stable or increase, open circles) at haulouts and rookeries in (*a*) 1985, (*b*) 1990, (*c*) 1995, and (*d*) 2000.



of the eastern stock, slightly increased in numbers during this period at a rate of 0.7% annually. Between 2000 and 2002, the Steller sea lion abundance of all surveyed sites increased for the first time since comprehensive surveys began.

Relationship between commercial groundfish and Steller sea lion trends

Similar to Steller sea lion population trends, fish densities varied across regions and years (Fig. 7). Walleye pollock, Pacific cod, and Atka mackerel were found in increasing abundance from east to west, while arrowtooth flounder was greatest in the Gulf of Alaska and Southeast Alaska. Temporal trends in biomass density varied by species and region. Differences were as much as a factor of 5, or 1.6 orders of magnitude (base e) (i.e., $5 = e^{1.6}$), between the minimum and maximum yearly mean fish densities. Dillingham et al. (2004) provided further detail regarding spatial and temporal differences in fish abundance.

We found negative associations between walleye pollock density and associated prevailing conditions and Steller sea lion abundance trends in all models ($P < 0.10$; Fig. 8; Table 1). Estimates for the magnitude of the observed relationship ranged from $\hat{\beta}_{fish} = -0.0181$ (SE = 0.0064) for the unadjusted model (eq. 6) to $\hat{\beta}_{fish} = -0.0079$ (SE = 0.0040) for the spatially and temporally adjusted model (eq. 8). Using eq. 12, a one order of magnitude (base e) decrease in walleye pollock abundance is expected to increase the annual rate of Steller sea lion population change (λ) by between (*i*) $\widehat{\Delta\lambda}/\lambda = \exp(-1 \times -0.0181) - 1 = 0.018$ (or ~1.8% if $\lambda = 1$) using the estimate from eq. 6 and (*ii*) $\widehat{\Delta\lambda}/\lambda = \exp(-1 \times -0.0079) - 1 = 0.0079$ (or ~0.8% if $\lambda = 1$) using the estimate from eq. 8. For example, mean walleye pollock density in the Gulf of Alaska ranged from a maximum of 4633.2 kg·km^{-2} in 1984 to a minimum of 955.0 kg·km^{-2} in 2001, a decrease of ln(4633.2) – ln(955.0) = 1.58 orders of magnitude (base e). Thus, the expected increase in λ across this decrease in walleye pollock density and affiliated factors is $\widehat{\Delta\lambda}/\lambda = \exp(-1.58 \times -0.0181) - 1 = 0.029$ (i.e., λ would increase to $(1 + 0.029)\lambda$). While this is a small portion of the variation seen in Steller sea lion population trends, it is not an inconsequential amount. However, in interpreting these regression results, it must be remembered that the walleye pollock density covariate represents more than walleye pollock abundance alone. The variable represents all the biotic and abiotic factors associated with increases or declines in walleye pollock density. The same can be said for the other species abundance variables.

The regression results also showed significant negative associations ($P < 0.10$) between Pacific cod density (and affiliated factors) and $\hat{r}$ in the unadjusted model (eq. 6; Table 1) and $\hat{r}$ in the model adjusted for region (eq. 7; Table 1). However, when adjusted for temporal trends by the addition of year into the model (eq. 8), the relationship between $\hat{r}$ and Pacific cod density was no longer significant ($P = 0.8898$). Additionally, Pacific cod density was not significant in multispecies models ($P > 0.10$ for all models). Pacific cod is a gadid, as is walleye pollock, and they were positively correlated ($r = 0.51$; $P < 0.0001$) at the locations studied. Thus, we place limited confidence in the relationships seen between Steller sea lion abundance trends and Pacific cod in eqs. 6–7.

No significant relationship was found between arrowtooth flounder density and $\hat{r}$ in any of the regression models (eq. 6, $P = 0.5368$; eq. 7, $P = 0.2544$; eq. 8, $P = 0.1712$). Also, no significant association between Atka mackerel density and Steller sea lion abundance trends was found in eq. 6 ($P = 0.5763$). Owing to the limited range of Atka mackerel, only locations in the Aleutian Islands were studied, so eq. 7 is equivalent to eq. 6. When adjusting for temporal trends (eq. 8), the relationship was significantly negative ($\hat{\beta}_{fish} = -0.0047$; SE = 0.0028; $P = 0.0925$). These results did not change with multispecies fish models (Dillingham et al. 2004).

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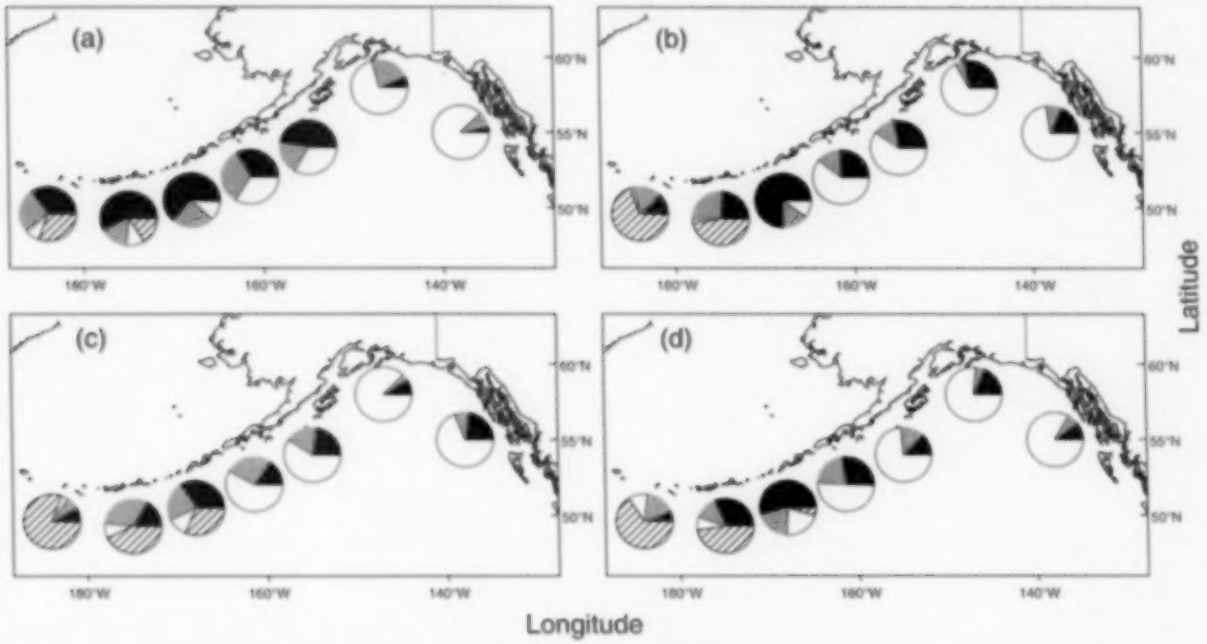
Fig. 7. Spatial trends in relative densities walleye pollock (*Theragra chalcogramma*, solid), Pacific cod (*Gadus macrocephalus*, shaded), arrowtooth flounder (*Atheresthes stomias*, open), and Atka mackerel (*Pleurogrammus monopterygius*, hatched) for (*a*) 1984–1986, (*b*) 1990–1991, (*c*) 1994–1996, and (*d*) 1999–2000.



Relationship between commercial fishing effort and Steller sea lion trends

Trawl and longline effort for vessels subject to the NPGOP program greater than 18.3 m in length was estimated near the 33 Steller sea lion cluster locations. There was considerable variation in the level and composition of fishing effort across regions (Fig. 9), as well as between cluster locations within a region. The highest levels of trawl effort were seen in the Aleutian Islands, followed by the Gulf of Alaska. There was relatively little trawl effort in Southeast Alaska, making up only 7.2% of fishing effort in the region, compared with 38% of fishing effort in both the Gulf of Alaska and the Aleutian Islands. The Aleutian Islands had the highest level of longline effort, while Southeast Alaska and the Gulf of Alaska had comparable levels of longline effort. The proportion of vessels >38.1 m increased from east to west. When classified by gear type and vessel length, there was a very strong relationship between fishing effort and catch (Pearson's correlation statistic >0.8 for all classifications). Trawl vessels had approximately 25 times the catch of a comparably sized longline vessel for the same number of days of effort, while larger vessels caught approximately twice as much biomass as smaller vessels for the same amount of effort.

There were statistically significant positive relationships seen between commercial trawl effort and Steller sea lion abundance trends (Table 2). However, the estimated effect size coupled with the range of measured trawl effort leads to the conclusion that the observed relationship between Steller sea lions and trawl effort has little biological importance. For example, the regionally and temporally adjusted model (eq. 9) estimates $\hat{\beta}_{trawl} = 0.000\ 028$; that is, the set of factors that might lead to 100 extra days of trawl effort is expected to increase the annual rate of Steller sea lion change by 0.28% from its current level (i.e., λ would increase to $(1 + 0.0028)\lambda$). Most locations (91%) had between 0 and 200 days of trawl effort. The expected difference in λ across this range of trawl effort is only 0.56% (i.e., λ would increase to $(1 + 0.0056)\lambda$). Estimates were similar with and without Southeast Alaska locations included. However, when the two locations with very high trawl effort (Sea Lion Rock near Amak Island and Akutan Island) were excluded from the analysis, there was no significant relationship between trawl effort and Steller sea lion population trends ($P = 0.34$).

Negative relationships were seen between longline effort and the instantaneous rate of Steller sea lion population change in all models (eqs. 9–11), but the relationships generally were not statistically significance ($P > 0.10$; Table 2). When Southeast Alaska was excluded from the model, a significant relationship was seen in the regionally adjusted model (eq. 10; $\hat{\beta}_{longline} = -0.000\ 034$; SE = 0.000 019; $P = 0.0738$). The relationship can be interpreted as the set of factors that might lead to 100 extra days of longline effort would decrease the annual rate of Steller sea lion change by 0.34% from its current level (i.e., λ would decrease to $(1 - 0.0034)\lambda$). Most locations (95%) had between 0 and 600 days of longline effort. The expected difference in λ across this range of longline effort is 2.0% (i.e., λ would change to $(1 - 0.020)\lambda$). While a 0.02 change in λ can have important biological consequences, it only explains a small portion of the historic trajectories seen in Steller sea lion population trends. Significant relationships were also seen when Sea Lion Rock and the Akutan Island vicinity were

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Fig. 8. Values of $\hat{\varepsilon}_{ijk}$ versus walleye pollock (*Theragra chalcogramma*) biomass density (ln(kg·km^{-2})) for (*a*) the unadjusted generalized estimation equations model ($\hat{\beta}_{\text{fish}} = -0.0181$; $P = 0.005$; eq. 6) and the generalized estimation equations model adjusted for region and year ($\hat{\beta}_{\text{fish}} = -0.0079$; $P = 0.049$; eq. 8) illustrated for (*b*) Southeast Alaska, (*c*) the Gulf of Alaska, and (*d*) the Aleutian Islands (year set at 1990 for illustrative purposes). Southeast Alaska, crosses; Gulf of Alaska, asterisks; Aleutian Islands, triangles.

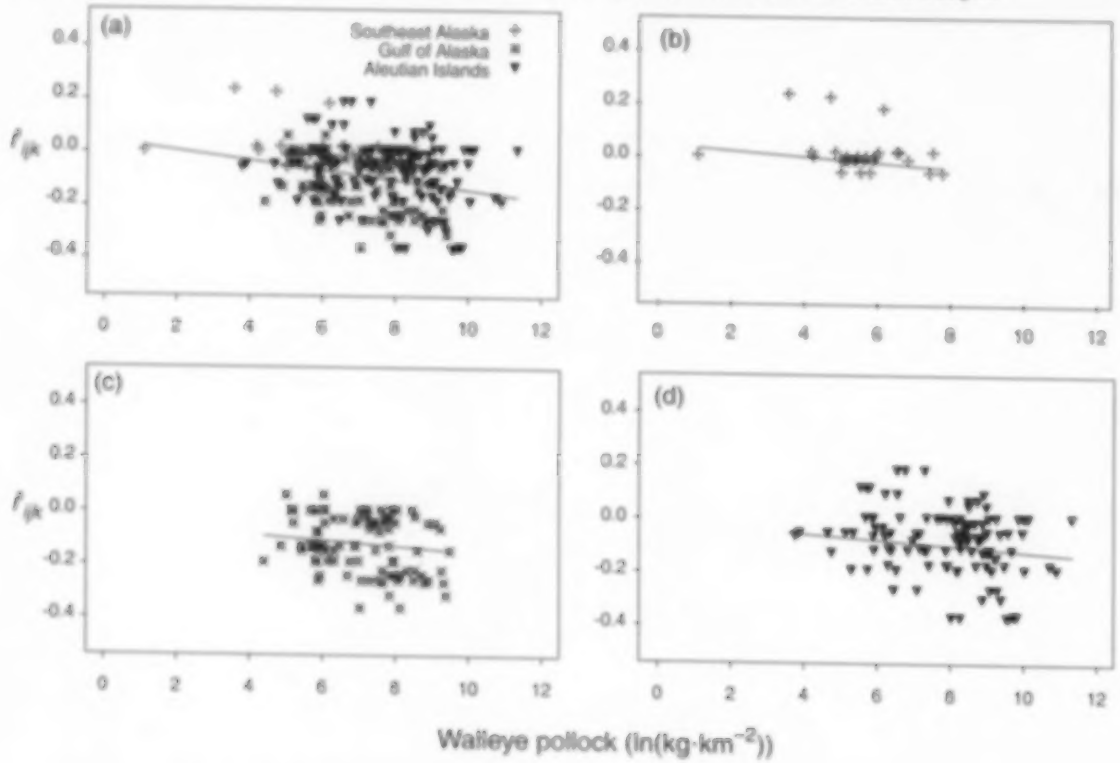

Table 1. Commercial groundfish density and Steller sea lion (*Eumetopias jubatus*) population trend regression results.

Model	$\hat{\beta}_{\text{fish}}$	SE	*P* value
Walleye pollock (*Theragra chalcogramma*)			
Unadjusted (eq. 6)	–0.0181	0.0064	0.0047
Region adjustment (eq. 7)	–0.0144	0.0055	0.0092
Region and temporal adjustment (eq. 8)	–0.0079	0.0040	0.0490
Pacific cod (*Gadus macrocephalus*)			
Unadjusted (eq. 6)	–0.0257	0.0084	0.0022
Region adjustment (eq. 7)	–0.0153	0.0082	0.0624
Region and temporal adjustment (eq. 8)	0.0008	0.0059	0.8898

Note: $\hat{\beta}_{\text{fish}}$, estimate for the magnitude of the observed relationship; SE, standard error.

excluded from the analyses for the unadjusted model (eq. 9; $\hat{\beta}_{\text{longline}} = -0.000\,050$; SE = 0.000 024; $P = 0.0388$) and the regionally adjusted model (eq. 10; $\hat{\beta}_{\text{longline}} = -0.000\,043$; SE = 0.000 022; $P = 0.0482$).

Discussion

This fine-scale geographic analysis found correlations at the local level between Steller sea lion population abundance trends and commercial groundfish density and commercial fishing effort (vessels >18.3 m). These covariates help explain some but not all of the differences in population trajectories between the various rookeries and haulout areas over time.

Of the four major commercial fish species analyzed from the bottom trawl survey data, only walleye pollock density had a consistent and statistically significant inverse relationship ($P < 0.10$) with the instantaneous rate of sea lion population change. The negative relationship suggests that as walleye pollock density increases, the rate of population

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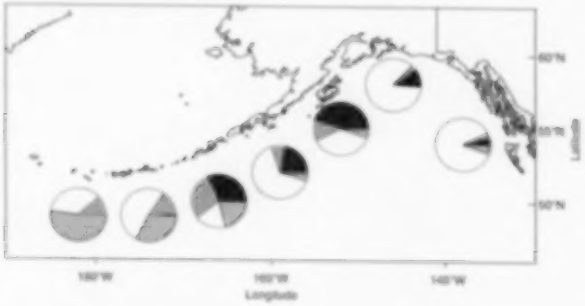
Table 2. Commercial fishing effort and Steller sea lion (*Eumetopias jubatus*) population trend regression results.

Model	$\hat{\beta}_{trawl}$	SE	*P* value	$\hat{\beta}_{longline}$	SE	*P* value
With Southeast Alaska						
Unadjusted (eq. 9)	0.000 018	0.000 008	0.0283	–0.000 032	0.000 021	0.1236
Region adjustment (eq. 10)	0.000 018	0.000 005	0.0005	–0.000 029	0.000 019	0.1222
Region and temporal adjustment (eq. 11)	0.000 028	0.000 007	0.0002	–0.000 021	0.000 018	0.2499
Without Southeast Alaska						
Unadjusted (eq. 9)	0.000 031	0.000 007	<0.0001	–0.000 018	0.000 020	0.3646
Region adjustment (eq. 10)	0.000 017	0.000 006	0.0025	–0.000 034	0.000 019	0.0738
Region and temporal adjustment (eq. 11)	0.000 027	0.000 008	0.0004	–0.000 024	0.000 019	0.2093

Note: $\hat{\beta}_{trawl}$ and $\hat{\beta}_{longline}$, estimates for the magnitude of the observed relationship; SE, standard error.

Fig. 9. Spatial differences in commercial fishing effort (days) by gear type and boat length (trawl, 18.3–38.1 m: solid; trawl, >38.1 m: shaded; longline, 18.3–38.1 m: open; longline, >38.1 m: hatched) for 1990–2002.



change ($r = \ln \lambda$) declines. However, the estimated change in λ of –0.029 across observed extremes in walleye pollock density suggests that these differences may account for only a small portion of the observed changes in Steller sea lion population trends in the last 20 years. Loughlin and Merrick (1988) and Ferrero and Fritz (1994) also examined the relationship between walleye pollock and Steller sea lion abundance. Using catch to estimate biomass, they were unable to discern a statistically significant relationship.

However, regression models are incapable of discerning whether walleye pollock density is a driving variable or merely correlated with some other environmental variable that is the driving force behind the Steller sea lion decline. An ocean regime shift in 1977 (Barange 2003; Beamish et al. 2004) produced an ecosystem favored by walleye pollock. Rosen and Trites (2000) and Trites and Donnelly (2003) suggest the shift to walleye pollock and a lessening of prey quality may play a role in the decline of Steller sea lion abundance. Current changes in climate suggest a return to conditions seen in the 1950s–1970s (Klyashtorin 1998), when Steller sea lion populations were high (Loughlin et al. 1992). This is coupled with evidence of smaller regime shifts in the north Pacific in 1989 and 1998 (Beamish et al. 2004) and the gradual stabilization of Steller sea lion populations. Differing effects of regime shifts on fisheries at a local scale (Beamish et al. 2004) could explain differences in the timing and scale of the Steller sea lion decline.

There were also indications of a relationship between fishing effort and the instantaneous rate of Steller sea lion population change. In general, abundant fish resources would both attract greater fishing effort and greater Steller sea lion abundance. However, competition for resources with fisheries may have a negative effect on marine mammals (Trites et al. 1997; DeMaster et al. 2001). In addition to the effect climate has on fish stocks (Klyashtorin 1998; Beamish et al. 2004), intensive fishing can drastically alter the structure of fish stocks and possibly lead to localized depletions (DeMaster et al. 2001), disruption of forage fishes (Sinclair and Zeppelin 2002), and decreased diversity (Barange 2003), which has been linked to Steller sea lion decline (Merrick et al. 1997). This study observed both positive and negative relationships between fishing effort and Steller sea lion trends with varying levels of significance.

Positive relationships were observed between Steller sea lion trends and trawl fishing effort. Trawl fishing is restricted to fishing at least 18.5 km from rookeries and haulouts. The positive relationship may be indicative of both the mutual attraction of fisheries and sea lions to areas of higher fish abundance and the efficacy of the 18.5 km exclusion zone for that fishery. On the other hand, negative relationships were detected between longline fishing effort and Steller sea lion trends. In the case of the longline fishery, the exclusive zone is as little as 5.5 km. Closer proximity and greater opportunity for interaction between the longline fishery and Steller sea lions may explain the negative relationship. However, once again the major decline in the Steller sea lion populations can not be explained by the estimated effect size of longline fishing. Across observed extremes in longline fishing effort, the estimated change in λ is approximately –0.02.

Whether these fishery factors may or may not be driving variables cannot be discerned from an observational study. Only a manipulative experiment conducted over multiple locales and over multiple years can actually assess whether the relationships we observed are simply correlative or actually causal. An adaptive management strategy tied to experimental manipulation and investigation may be the only way to verify our results. Our findings suggest the factors we investigated have a relatively small incremental effect on Steller sea lion trends — in most cases, much smaller than the rates of decline seen in the 1970s and 1980s, when the western stock declined by more than 10% annually. If our results are correct, a manipulative experiment, for instance, using the longline fishery would need to compare a sixfold difference in fishing effort to see less than a 0.02 change in λ. Hence,

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any effective, manipulative experiment would need to test treatment extremes in order to have a chance of detecting impacts on Steller sea lion population trends.

There are likely to be future impacts of commercial fishing activity on marine mammals (DeMaster et al. 2001), with marine mammals and commercial fisheries competing for a limited supply of primary production (Trites et al. 1997). Therefore, additional understanding of marine mammal – fisheries interactions is required (Read and Wade 2000). There is also increasing evidence of the effect regime shifts have on fisheries (Klyashtorin 1998; Barange 2003; Beamish et al. 2004), and the effect can differ on a localized scale (Beamish et al. 2004). The statistical methods used in this study to examine the fine-scale, geographic, fisheries – marine mammal interactions can be applied to other populations as well. Census data are available for a variety of marine mammals (Read and Wade 2000), with varying levels of accuracy (Trites et al. 1997), and experimental trawl or commercial catch data are also available in many locations. Through careful examination of both localized trends and fine-scale interactions, there is the possibility to assess anthropogenic effects on wild resources in the absence of deliberate experimentation. The opposing demographic trends of the localized populations provide a basis of comparison when manipulative controls are cost-prohibitive or difficult to achieve.

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Effects of riffle–step restoration on hyporheic zone chemistry in N-rich lowland streams

Tamao Kasahara and Alan R. Hill

Abstract: Stream restoration projects that aim to rehabilitate ecosystem health have not considered surface–subsurface linkages, although stream water and groundwater interaction has an important role in sustaining stream ecosystem functions. The present study examined the effect of constructed riffles and a step on hyporheic exchange flow and chemistry in restored reaches of several N-rich agricultural and urban streams in southern Ontario. Hydrometric data collected from a network of piezometers and conservative tracer releases indicated that the constructed riffles and steps were effective in inducing hyporheic exchange. However, despite the use of cobbles and boulders in the riffle construction, high stream dissolved oxygen (DO) concentrations were depleted rapidly with depth into the hyporheic zones. Differences between observed and predicted nitrate concentrations based on conservative ion concentration patterns indicated that these hyporheic zones were also nitrate sinks. Zones of low hydraulic conductivity and the occurrence of interstitial fines in the restored cobble–boulder layers suggest that siltation and clogging of the streambed may reduce the downwelling of oxygen- and nitrate-rich stream water. Increases in streambed DO levels and enhancement of habitat for hyporheic fauna that result from riffle–step construction projects may only be temporary in streams that receive increased sediment and nutrient inputs from urban areas and croplands.

Résumé : Les projets de restauration des cours d'eau pour la réhabilitation de la santé de l'écosystème ne tiennent pas compte des liens entre les eaux superficielles et souterraines, bien que l'interaction entre l'eau du cours d'eau et l'eau d'origine phréatique joue un rôle fondamental dans le maintien des fonctions des écosystèmes d'eau courante. Notre étude examine l'effet de la construction de rapides et d'un seuil sur les échanges de débits et sur la chimie des eaux dans des sections restaurées de plusieurs cours d'eau agricoles et urbains riches en N dans le sud de l'Ontario. Des données hydrométriques récoltées à l'aide d'un réseau de piézomètres et l'utilisation de traceurs conservateurs indiquent que les rapides et les seuils artificiels favorisent efficacement les échanges hyporhéiques. Toutefois, malgré l'utilisation de cailloux et de pierres dans la construction des rapides, les fortes concentrations d'oxygène dissous (DO) du cours d'eau sont rapidement épuisées à mesure qu'on s'enfonce dans les zones hyporhéiques. Les différences entre les concentrations prévues et observées de nitrates basées sur des patrons conservateurs de concentrations ioniques indiquent que ces zones hyporhéiques sont aussi des trappes à nitrates. L'existence de zones de faible conductivité hydraulique et la présence de particules fines dans les couches restaurées de cailloux–pierres laissent croire que l'envasement et le colmatage du lit du cours d'eau peuvent réduire la pénétration en profondeur de l'eau courante riche en oxygène et en nitrates. Les accroissements des concentrations de DO du lit et l'amélioration de l'habitat de la faune hyporhéique qui résultent des projets de construction de rapides et de seuils peuvent n'être que passagers dans les cours d'eau qui reçoivent des apports élevés de sédiments et de nutriments des zones urbaines et agricoles.

[Traduit par la Rédaction]

Introduction

The hyporheic zone is the saturated subsurface zone beneath and adjacent to a stream channel that interacts with stream water (White 1993). This zone is commonly defined as the zone that contains >10% stream water and <90% groundwater (Triska et al. 1989). Stream–subsurface water interactions have been a major focus of research in the past two decades (Jones and Mulholland 2000). The hyporheic zone is a habitat for stream invertebrates (Williams 1993) and provides preferential spawning gravels for salmonid species (Baxter and Hauer 2000). Hyporheic exchange flow enhances the mass transfer of dissolved solutes and particulates between the stream and the streambed, and the transformation and retention of nutrients, organic matter, and trace metal occurring in the hyporheic zone is important for stream ecosystem function (Findlay et al. 1993; Valett et al. 1996; Fuller and Harvey 2000). Many studies have exam-

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Table 1. Study site descriptions.

	Rouge T1	Rouge T2	Silver Creek	
Channel width (m)	1.5	1.2	7	
Channel gradient ($m \cdot m^{-1}$)	0.01	0.01	0.003	
Summer baseflow ($L \cdot s^{-1}$)	9	16	344	
Constructed feature	Riffle	Step	Riffle	
			Constructed	Natural
Study reach length (m)	5	6	55	30
Riffle length (m)	3		40	15
LHG ($m \cdot m^{-1}$)	0.036	0.29	0.015	0.005

Note: LHG, longitudinal head gradient along the features.

ined nutrient transformation processes in hyporheic zones with particular focus on nitrogen dynamics (Triska et al. 1989; Hill et al. 1998; Storey et al. 2003*a*). Jones and Holmes (1996) have proposed a conceptual model suggesting that low dissolved oxygen concentrations in the streambed and high nitrate levels in agricultural and urban streams result in a hyporheic zone that functions as a sink of nitrate where denitrification is the major nitrogen transformation process (Hill et al. 1998).

Current knowledge of the functional role of stream hyporheic zones is based mainly on studies of relatively undisturbed streams, and it is important to focus greater attention on the impact of human activities on surface–subsurface interactions in agricultural and urban streams (Pringle and Triska 2000; Hancock 2002; Lefebvre et al. 2004). Many lowland streams have been extensively altered by channelization, and channel restoration to rehabilitate damaged or degraded reaches of these streams has become an important aspect of stream management in recent decades (Osborne et al. 1993; Brookes and Shields 1996).

Channel restoration projects are used to stabilize channels, control bank erosion, and enhance the quality of aquatic habitat by modifying instream structures (Sear 1994; Kondolf 1995). Frequently used methods are the placement of boulders, the construction of deflectors and riffles, and channel remeandering at a larger scale (Nielsen 1996; Brookes 1996). These channel features have been identified as an important driving force of hyporheic exchange in natural streams (Harvey and Bencala 1993; Vervier et al. 1993; Kasahara and Wondzell 2003). The reinstatement of relatively coarse substrates that do not erode during bankfull flow events is also a common practice (Brookes 1996). The coarse substrate may enhance stream–subsurface water exchange and, in turn, the transfer of dissolved solutes from the stream to the streambed. Thus, although restoration projects are often designed to improve instream habitat structures, these projects are also likely to enhance hyporheic function in stream ecosystems. The restoration of channel morphologic features and the addition of coarse substrates constitute valuable manipulation experiments that can increase our understanding of hyporheic exchange processes. Studying these morphologic features in the context of the hyporheos can also provide valuable information for the improvement of stream restoration techniques.

Natural riffle-pool and step-pool sequences have received most attention among the range of channel morphological features that exert a strong control on hyporheic exchange (Sterba et al. 1992; Harvey and Bencala 1993; Storey et al. 2003*b*). Hyporheic exchanges driven by these channel features have a relatively short residence time (Harvey and Wagner 2000) and may account for a large portion of hyporheic exchange in many stream reaches (Kasahara and Wondzell 2003). The present study examines hyporheic exchange flow and subsurface chemistry induced by constructed riffles and steps, which are one of the most common procedures used in channel restoration projects. The objectives of the research were to examine (*i*) the stream–subsurface water interaction induced by constructed riffles and steps and (*ii*) the patterns of subsurface chemistry with particular focus on oxygen and nitrate dynamics in the hyporheic zone. We hypothesize that constructed riffles and steps enhance hyporheic exchange and expand the zone of increased oxygen and nitrate concentrations in the streambed. Our approach involved a comparison of the hyporheic zone beneath a large constructed riffle and a natural riffle at one study site and analysis of a small constructed riffle and step in two other streams. Hydrometric data collected from piezometer nests and conservative tracer releases were combined to examine stream–subsurface exchanges and reactive element dynamics.

Materials and methods

Study sites and restoration

Three study sites with a recently restored riffle or step were located on streams near Toronto, Ontario, Canada. One of the study sites was on Silver Creek, a fifth-order tributary of the Credit River, approximately 50 km west of Toronto (Table 1). The study site was in the lower portion of the watershed, downstream from the rapidly expanding urban centre of Georgetown. At this location, the stream flows across a 70 m wide grass-vegetated floodplain within a deep valley eroded in fine-textured glacial till. The floodplain is surrounded by residential areas and several major roads, and elevated concentrations of NO_3-N and Cl^- were found in stream water. A constructed riffle and a natural riffle were examined in this study reach (Table 1). A large riffle was constructed in 1997 using cobbles and boulders with diameters ranging from 0.15 to 0.45 m. The thickness of the cobble–boulder layer was about 0.6 m (Fig. 1*a*). Before the restoration, three naturally occurring riffle-pool sequences were present in the reach. The natural riffle studied was located about 80 m upstream from the constructed riffle and had a sandy gravel bed with some cobbles that ranged in

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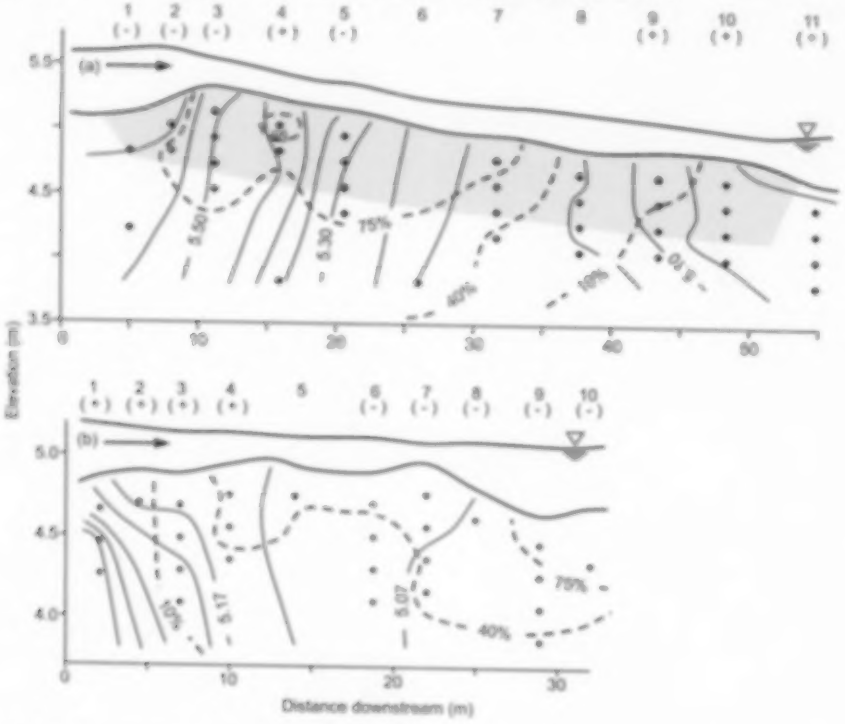
Fig. 1. Observed hydraulic heads (solid line) and fraction of stream water (broken line) at (*a*) the constructed riffle and (*b*) the natural riffle in Silver Creek. Hydraulic heads are from the 15 August 2003 sampling date. The stream water fraction was calculated from a two-component mixing equation using mean stream water and groundwater Cl^- concentrations in July–October 2003. Numbers above represent piezometer nest locations; symbols under the numbers indicate downwelling (–) and upwelling (+); ◆ indicates piezometers. Shaded area indicates the cobble–boulder layer. The underlined triangle indicates the water table.



diameter from 0.08 to 0.2 m. The surface boulders and cobbles were covered by lime-encrusted algal mats dominated by *Cladorphra* in both riffles.

The other two study sites were on headwater tributaries of the Rouge River, approximately 20 km north of Toronto on the southern slope of the Oak Ridges moraine. The unconfined aquifer formed in the Oak Ridge moraine extends up to 15 m thick and discharges groundwater to the tributaries. The stream channels have been straightened in past decades, and areas of residential development and agricultural fields surround the study reaches. The stream water at these sites had relatively high NO_3-N concentrations.

In the Rouge River tributary 1 (Rouge T1) site, a small riffle was constructed in late August 2001 in a reach shaded by bankside deciduous trees (Table 1). The restoration project added a layer of cobbles to the channel that was 0.2 to 0.25 m thick at the crest of the riffle and 0.05 to 0.1 m thick in the rest of the reach (Fig. 2*a*). The diameter of the cobbles ranged from 0.05 to 0.12 m, whereas the original substrate was sandy gravel.

In Rouge River tributary 2 (Rouge T2) site, a small step was constructed in August 2001 by placing a 0.17 m diameter log normal to the stream flow and supporting the log with boulders at the sides of the channel (Table 1). A sheet fabric with low hydraulic conductivity was installed on the streambed extending 1 m upstream from the log to prevent erosion (Fig. 2*b*). The substrate was not manipulated at this site. Before the restoration, the study reach was a long glide with no riffle or step structures. The substrate of the study reach was sandy gravel underlaid by a low conductive layer of sandy loam. A stand of eastern white cedar (*Thuja occidentalis*) extends along the banks shading the channel.

Methods

Water sampling and measurements

A longitudinal transect of piezometer nests was installed at intervals in the channel along the riffles and step to measure hydraulic head and subsurface water chemistry. Each nest consisted of polyvinyl chloride (PVC) pipes with an inside diameter of 1 cm. Piezometers at Silver Creek sites had a 5 cm slot zone and were inserted at depths of 0.2–0.25, 0.4–0.45, 0.6–0.65, and 0.8–0.85 m (Fig. 1). Piezometers damaged in spring floods were replaced in early June 2003, and additional piezometers were installed, including two at a depth >1.0 m at the constructed riffle site. At the two Rouge River tributary sites, a 3 cm slot zone at the bottom of the piezometers was placed at depths of 0.05–0.08, 0.1–0.13, 0.2–0.23, and 0.6–0.63 m (Fig. 2).

The location and elevation of piezometer nests and streambed were surveyed and mapped to scale using a total surveying station. Water sampling for chemistry and measurement of hydraulic heads were conducted during baseflow at approximately monthly intervals in May–October

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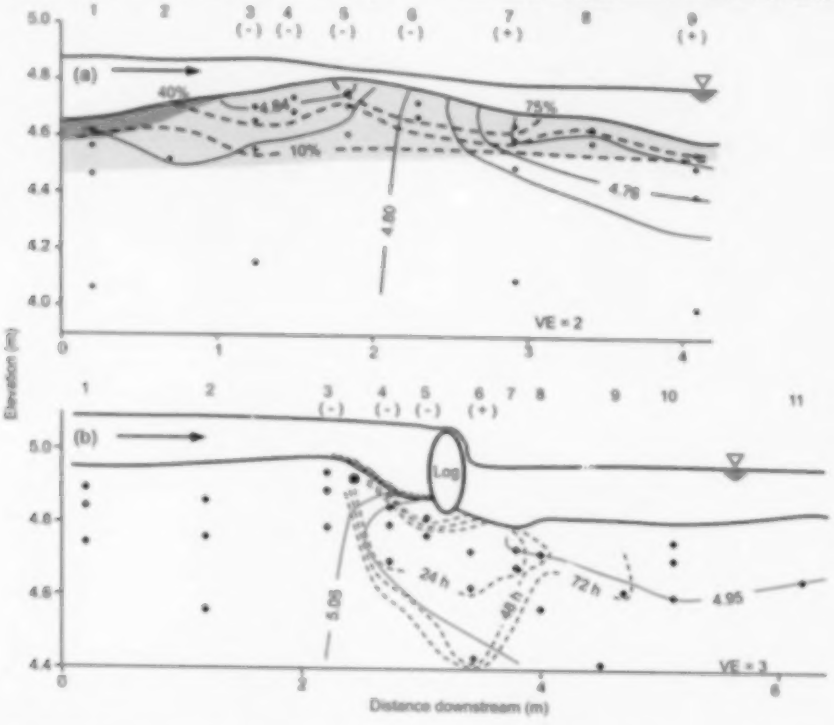
Fig. 2. Hydraulic characteristics at the Rouge River tributary sites. (*a*) Hydraulic heads observed on 24 June 2003 (solid line) and fraction of stream water (broken line) calculated using Br^- concentrations after 6.5 h of a stream tracer injection in a two-component mixing equation in Rouge T1 site. (*b*) Hydraulic heads observed on 22 October 2003 (solid line) and the extent of injected Br^- plume over time (broken line) in Rouge T2 site. Numbers above represent piezometer nest locations; symbols under the numbers indicate downwelling (–) and upwelling (+); ◆ indicates piezometers. VE indicates vertical exaggeration. Dark shaded area indicates the silt accumulation zone. Lighter shaded area indicates the cobble layer. The underlined triangle indicates the water table.



2002–2003. All piezometers were emptied and allowed to refill just before sampling. A small volume of water, 20 mL for the Silver Creek site and 10 mL for the Rouge River tributary sites, was slowly removed from the piezometers using a syringe. Samples were analyzed within 24 h for NO_3-N and later for chloride concentrations. Dissolved oxygen (DO) concentrations were measured in the field using a portable DO meter on two or three dates in June–August 2003. Water samples were collected with nylon tubing using a three-way stopcock connected to a syringe to prevent contact with ambient air during removal. The oxygen probe was then directly inserted into the syringe. Water was also sampled for analysis of ammonium (NH_4-N) and dissolved organic carbon (DOC) on one or two dates in June–October 2003. Nitrate, ammonium, and chloride were all analyzed using standard techniques for automated wet chemistry on a Technicon Auto-analyzer (American Public Health Association 1989). Detection limits for NO_3-N and NH_4-N were 0.003 mg·L^{-1}. DOC analysis was performed using a Shimadzu TOC-5050 Analyzer (Shimadzu Scientific Instruments Inc., Columbia, Maryland).

Solute injections

Short-term solute injections (Stream Solute Workshop 1990) were conducted to examine the extent of stream–subsurface water interaction and retention of nitrate as stream water flowed through the hyporheic zone in the Rouge tributary sites. In the Rouge T1 site, concentrated solutions of a conservative tracer, NaBr, and a biologically reactive tracer, KNO_3, were co-injected into the stream, 20 m upstream from the study reach in an area of turbulent mixing for 7 h on 23 July 2003. Background concentrations of Br^- in the stream and the streambed were <0.3 mg·L^{-1}, and stream concentration was raised to 10 mg·L^{-1} during the experiment. The tracer injection increased stream water NO_3-N concentrations from 0.11 to 0.2 mg·L^{-1}. Stream and subsurface water were sampled after 1 h and then at approximately 2 h intervals during the experiment. Water samples were analyzed for Br^- and NO_3-N in the lab. Bromide analysis was performed using an electrometric method with an Orion Research 720A Ion-analyzer (Orion Research, Cambridge, Massachusetts). The probe was cleaned and recalibrated frequently with standards. Measurements of samples were repeated during the analysis to check for consistency of values.

A short-term solute injection was not conducted at the Rouge T2 site because access was not feasible to the area upstream from the site. Instead, 100 g of NaBr and 40 g of KNO_3 were slowly injected into the streambed in a solid state as a powder over a 2 h period on 23 October 2003. Three injection pipes consisting of 1 cm diameter PVC pipes were installed 0.3 m apart perpendicular to stream flow and

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about 1 m upstream from the constructed step. These injection points were located in the area where hydraulic heads measured from piezometers indicated downwelling. The injection slot zone was located at 0.02–0.05 m below the streambed surface. Stream and subsurface water was sampled at 24 h intervals for 3 days, and the samples were analyzed for Br^- and NO_3-N in the lab. Water samples were also collected before the injection to obtain background concentrations.

Extent of the hyporheic zone

The interstitial zone containing >10% stream water was identified by using a two-component chemical mixing equation to calculate the fraction of stream water present in pore water based on conservative ion concentrations in stream water and groundwater. Background Cl^- was used for the Silver Creek riffles where groundwater and stream water had considerably different concentrations. Stream water and groundwater Cl^- concentrations were not significantly different at the Rouge T1 site, and stream water fraction in the subsurface was calculated using the plateau concentrations of the Br^- tracer at various sediment depths in the two-component mixing equation.

Statistical analysis

Hyporheic data were not normally distributed and a nonparametric Mann–Whitney *U* test was used to test for significant differences in NO_3-N and DO between natural and constructed riffles. Surface water and groundwater Cl^- concentrations were normally distributed, and means were compared with a *t* test. Levels of significance were set at $\alpha = 0.05$ for all statistical tests.

Results

Streambed hydrology

The subsurface hydrology of the sites has been documented in detail by Kasahara and Hill (2006). Briefly, the hydraulic heads revealed downwelling of stream water around piezometer nests 1–5 and upwelling at nests 9–11 in the Silver Creek constructed riffle site during baseflow in the 2-year study period (Fig. 1*a*). The mean (±SD) stream water Cl^- concentration of 125 (±4.0) mg·L^{-1} for sampling days in July–October 2003 was four times greater than the mean groundwater Cl^- concentration of 35 (±6.6) mg·L^{-1} ($P < 0.001$, *t* test). The mixing equation based on Cl^- suggested that the depth of >40% stream water zone extended >1.4 m at nests 1–6, whereas nests 8–11 had ≤25% stream water (Fig. 1*a*). The low stream water fractions at nests 9–11 indicate the presence of localized groundwater upwelling. In the Silver Creek natural riffle site, a strong localized groundwater upwelling was apparent at nests 1–4 in May–October 2002–2003, and the zone of stream water downwelling was restricted to nests 6–10. The mixing equation using background Cl^- suggested that < 0% stream water was present at nests 1–2, whereas a zone of >40% stream water extended to depths of 0.6–0.8 m at nests 7–10 (Fig. 1*b*), agreeing with the upwelling–downwelling trend indicated by the observed hydraulic heads.

In Rouge T1 site, downwelling at nests 3–6 and upwelling at the riffle tail were indicated by the observed hydraulic heads in May–October 2003 (Fig. 2*a*). The fraction of stream water in the subsurface was calculated using the concentrations of injected Br^- after 6.5 h in a stream tracer experiment. The Br^- concentration in the piezometers did not change between 5 h and 6.5 h, indicating that a plateau concentration had been reached. The zone of >10% stream water extended >0.2 m depth at the riffle crest and <0.1 m at the upstream and downstream end of the study reach, which is consistent with the hyporheic flow path indicated by the hydraulic heads (Fig. 2*a*). Shallow depths at nests 5–7 had >75% stream water, and this zone coincided with the zone where Br^- was first detected after 1 h of stream enrichment, suggesting a short residence time of hyporheic exchange flow.

A zone of strong downwelling with a vertical head gradient (VHG) greater than –0.8 m·m^{-1} occurred just upstream from the constructed step at the Rouge T2 site on all sampling dates, and a slight upwelling was observed at nest 6 (Fig. 2*b*). Bromide was injected as a powder into the streambed at this site, and the fractions of stream water were not estimated. However, the pattern of Br^- transport was consistent with the downwelling and upwelling trends indicated by the hydraulic heads (Fig. 2*b*). The movement of Br^- was dominated by downstream flow. The boundary of the tracer plume had reached nest 7 by 24 h and nest 8 by 48 h. The horizontal velocity of ~0.02 m·h^{-1} was relatively consistent during the experiment. The tracer also moved vertically, especially at the step, and a small concentration of tracer was detected at 0.4 m beneath the step (Fig. 2*b*).

Hyporheic chemistry patterns

The groundwater zone in the Silver Creek sites was identified as the upwelling zones of deeper water where chloride concentrations suggested the presence of <10% stream water (Fig. 1). Stream DO concentrations in Silver Creek were 9.6–11.6 mg·L^{-1}, whereas groundwater DO concentrations were relatively low, ranging from 0.7 to 2.5 mg·L^{-1} (Fig. 3). Although the DO level of the stream water was high, it decreased rapidly with depth in the streambed, and the nonparametric Mann–Whitney *U* test indicated that hyporheic DO concentrations for all sampling locations in the constructed and natural riffle were not significantly different. The rate of DO decrease was steeper in the constructed riffle in 2003 than in 2002 (Fig. 3). The zone of >2.0 mg·L^{-1} DO extended from nests 1 to 7 up to 0.6 m in depth in 2002, whereas >2.0 mg·L^{-1} DO was observed only at nest 5 in 2003.

Stream water NO_3-N concentrations in Silver Creek varied from 1.1 to 1.7 mg·L^{-1} during baseflow periods in 2002–2003. Groundwater NO_3-N concentrations in the constructed riffle showed a progressive increase from <0.05 mg·L^{-1} at nest 9 to 0.2–0.5 mg·L^{-1} at nests 10–11 (Fig. 4). In contrast, groundwater NO_3-N concentrations at nests 1–2 in the natural riffle were <0.01 mg·L^{-1}. Nitrate-N concentration rapidly declined with depth in the hyporheic zone, but the zone of >75% stream water in the constructed riffle showed a more gradual decline compared with rest of the hyporheic zone. Nests 3–5 retained >0.5 mg·L^{-1} NO_3-N up to a depth of 0.8 m in both 2002 and 2003 (Fig. 4). In the natural riffle, the zone of >0.5 mg·L^{-1} NO_3-N extended only to a depth of <0.4 m at nest 7 and did not coincide with the zone of >75%

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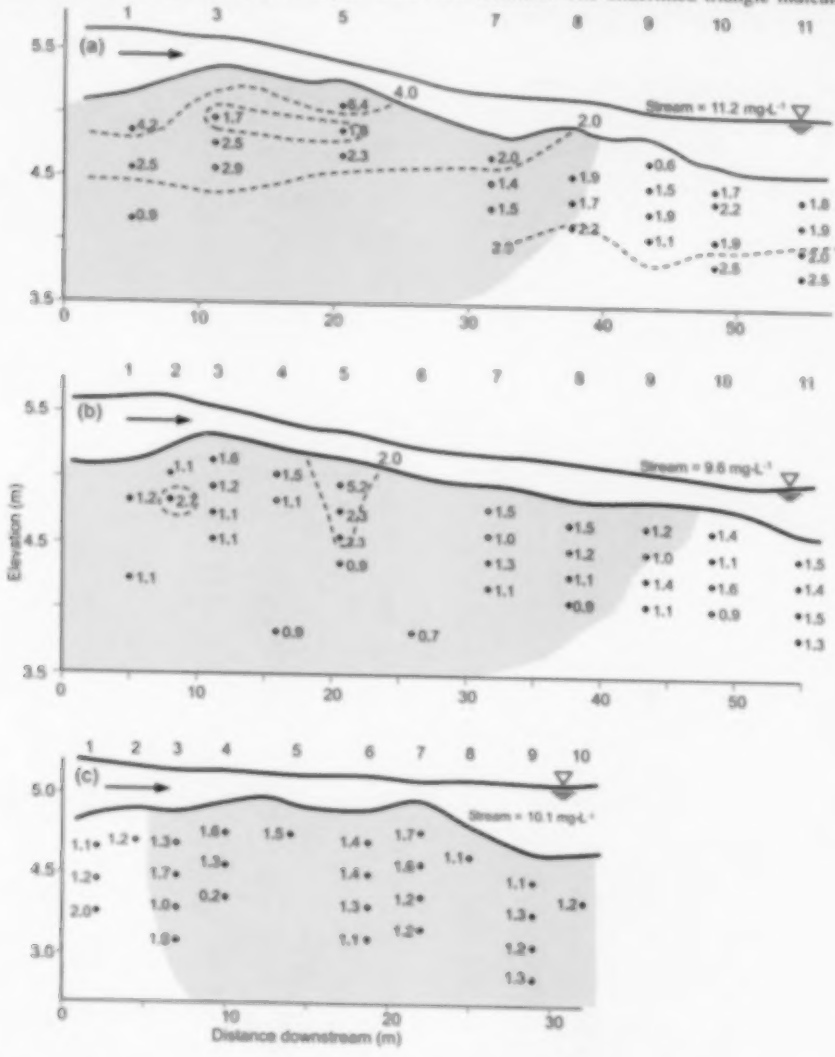
Fig. 3. (*a*) Dissolved oxygen concentrations (mg·L^{-1}) on 26 August 2002 in the constructed riffle; (*b*) mean values in July–August 2003 in the constructed riffle; and (*c*) mean values in July–August 2003 in natural riffle in Silver Creek. Shaded area indicates the zone with >10% stream water. Numbers above represent piezometer nest locations. The underlined triangle indicates the water table.



stream water. The Mann–Whitney test indicated that NO_3-N concentrations were significantly higher ($n_1 = 22$, $n_2 = 25$, $U = 439$, $p < 0.001$) in the hyporheic zone in the constructed riffle than in the hyporheic zone in the natural riffle.

The NH_4-N concentrations of stream water in Silver Creek were <0.02 mg·L^{-1}, whereas groundwater ranged from <0.01 to 0.9 mg·L^{-1}. In the hyporheic zone, NH_4-N concentrations (<0.01–1.0 mg·L^{-1}) were similar to the range of groundwater values, and there was no clear pattern of variation in concentrations with depth and distance downstream (Fig. 5). The zone with >0.5 mg·L^{-1} NO_3-N in the constructed riffle had lower NH_4-N concentrations, often <0.01 mg·L^{-1}, than elsewhere in the hyporheic zone (Fig. 5). Silver Creek stream water DOC concentration on 6 October 2003 was 4.7 mg·L^{-1} and groundwater DOC concentrations varied between 0.6 and 4.1 mg·L^{-1}. The DOC concentrations in the hyporheic zone did not show any trends with depth and distance downstream and ranged from 3.2 to 7.2 mg·L^{-1} and from 0.9 to 7.6 mg·L^{-1} in the constructed and natural riffles, respectively (Fig. 5).

In the Rouge T1 site, the DO concentration of stream water was 8.9 mg·L^{-1}, and values decreased with depth in the streambed, ranging from 3.2 to 6.3 mg·L^{-1} in the hyporheic zone to <3.0 mg·L^{-1} in groundwater on 24 June 2003 (Fig. 6*a*). The zone of >4.0 mg·L^{-1} DO was located within the constructed cobble layer. Similar DO patterns were observed in May and August 2002. The stream NO_3-N concentration varied from 0.1 to 0.2 mg·L^{-1} in 2002 and 2003, whereas groundwater concentration measured in the piezometers at ≥0.6 m depth was frequently <0.01 mg·L^{-1}. Nitrate-N concentration declined rapidly with depth in the hyporheic zone except in the zone of >75% stream water,

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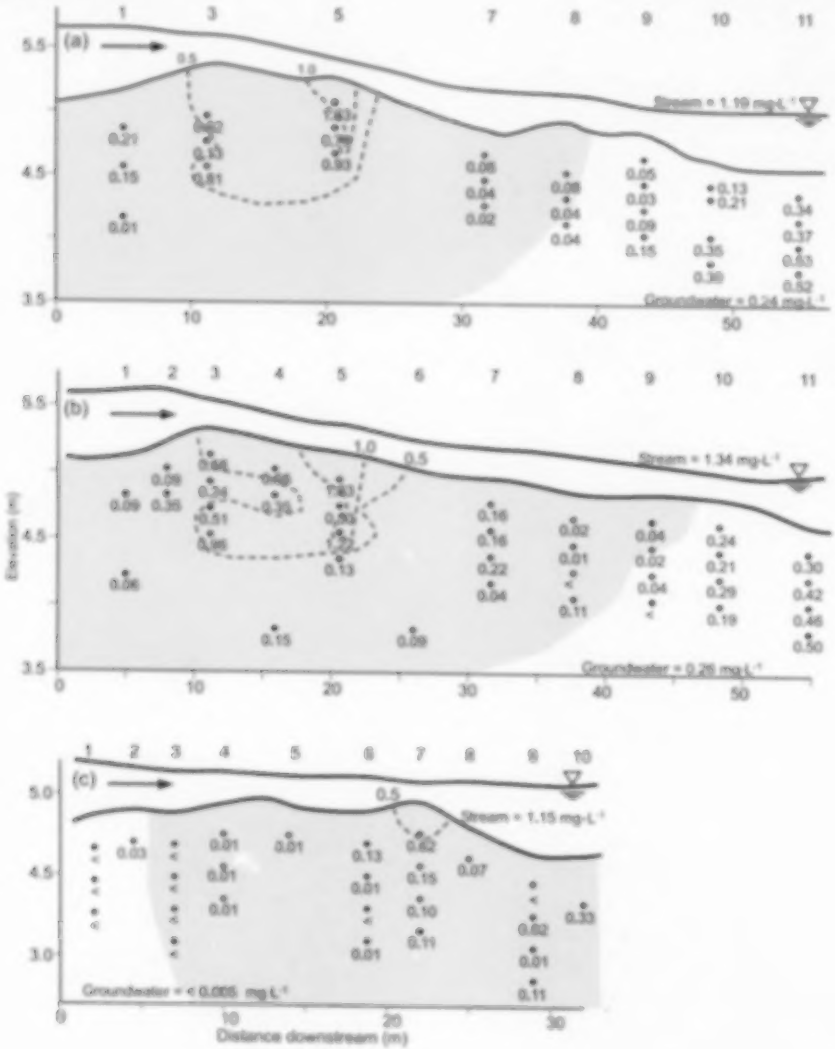
Fig. 4. Mean observed NO_3-N concentration (mg·L^{-1}) during baseflow at (*a*) the constructed riffle in August–October 2002, (*b*) the constructed riffle in July–October in 2003, and (*c*) the natural riffle in July–October in 2003 in Silver Creek. "<" indicates <0.01 mg·L^{-1}. Shaded area indicates the zone with >10% stream water. Numbers above represent piezometer nest locations. The underlined triangle indicates the water table.



where concentrations were >0.09 mg·L^{-1} NO_3-N at depths of 0.05–0.1 m (Fig. 6*b*).

The NH_4-N concentration of groundwater at the Rouge T1 site was 0.2–0.4 mg·L^{-1} and was considerably higher than the stream concentration of 0.02 mg·L^{-1}. In the hyporheic zone, the concentration ranged from 0.11 to 2.44 mg·L^{-1}, and there was no apparent vertical or longitudinal trend (Fig. 6*c*). Concentrations of DOC were sampled on 6 October 2003 and showed similar levels in stream water (4.1 mg·L^{-1}), groundwater (4.7 mg·L^{-1}), and the hyporheic zone (3.5–6.0 mg·L^{-1}).

The DO concentration of the stream water in the Rouge T2 site was 9.0 mg·L^{-1}, and concentrations declined within 0.1 m depth to ≤4.0 mg·L^{-1} at most piezometer nests on 24 June 2003 (Fig. 7*a*). Similar patterns were observed in July 2002. The zone just upstream from the constructed step showed higher DO concentrations of >5.0 mg·L^{-1} DO at nests 4 and 5. The stream water NO_3-N concentration fluctuated between 0.6 and 0.8 mg·L^{-1} and declined with depth in the streambed (Fig. 7*b*). The strong downwelling zone just upstream of the log showed a more gradual decline than other zones and had ≥0.4 mg·L^{-1} NO_3-N at ≤0.1 m depth (Fig. 7*b*). Stream water NH_4-N concentrations were considerably lower than the concentrations in the streambed, with the exception of the downwelling zone at nest 5 (Fig. 7*c*). The zone downstream from the strong stream water downwelling zone at nests 4 and 5 may have been influenced by the stream water, resulting in lower NH_4-N concentrations

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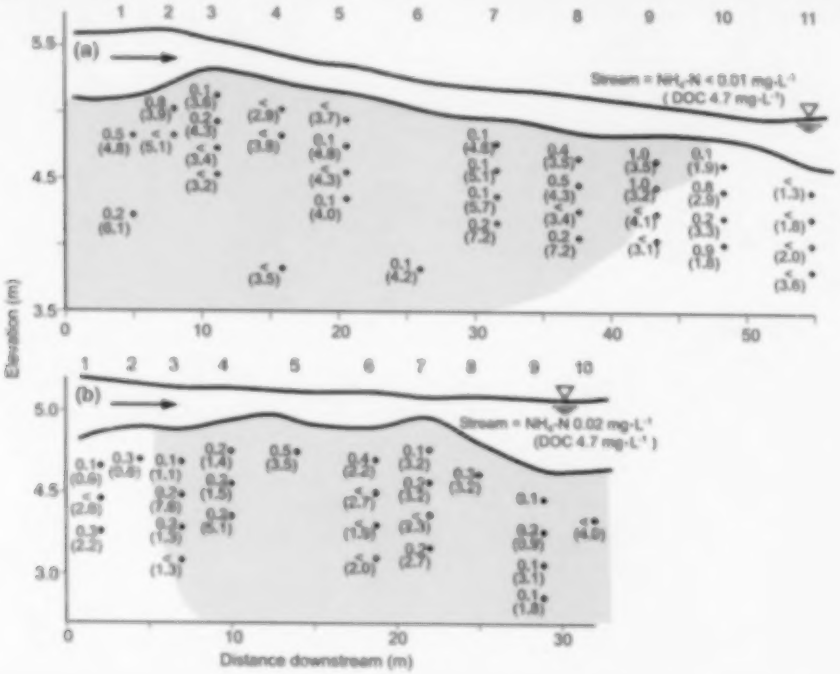
Fig. 5. Ammonium (NH_4-N) and dissolved organic carbon (DOC) concentrations ($mg \cdot L^{-1}$) on 6 October 2003 at (*a*) the constructed riffle and (*b*) the natural riffle in Silver Creek. "<" indicates <0.1 $mg \cdot L^{-1}$. Shaded area indicates the zone with >10% stream water. The underlined triangle indicates the water table.



compared with upstream piezometer nests 1–3 (Fig. 7*c*). Stream water DOC concentration was 9.1 $mg \cdot L^{-1}$ on a June 2002 sampling date, and the values in the streambed ranged from 3.9 to 16.4 $mg \cdot L^{-1}$.

DO and nitrate depletion in the hyporheic zone

Background Cl^- and injected Br^- concentrations indicated penetration of stream water into the streambed at the constructed riffles in the Silver Creek and Rouge T1 sites (Figs. 1 and 2*a*). If transport of reactive elements was similar to these conservative ions, then observed concentrations of DO and NO_3-N should be similar to concentrations predicted from the fraction of stream water and groundwater at various depths. However, DO and NO_3-N concentrations did not extend into the streambed as deeply as the conservative ions, and the observed concentrations were always lower than predicted.

If there was no uptake of DO in the constructed riffle at Silver Creek, the zone of >75% stream water, which extends to >0.8 m depth at nests 3–5, should have >7.0 $mg \cdot L^{-1}$ DO. In contrast, DO concentrations declined to <2.0 $mg \cdot L^{-1}$ within 0.2 m depth except at nest 5 (Fig. 3). In the natural riffle, predicted DO concentrations were >4.5 $mg \cdot L^{-1}$ DO in the zone of >40% stream water, whereas observed DO levels ranged from 0.2 to 1.7 $mg \cdot L^{-1}$ in the hyporheic zone. A similar trend occurred in the Rouge T1 site. If there was no consumption of DO, the zone of >75% stream water at nests 5–7 (0.05–0.1 m depth) should have >6.5 $mg \cdot L^{-1}$ DO, but values of ≤5.0 $mg \cdot L^{-1}$ were measured in this zone (Fig. 6*a*). Thus, DO was rapidly consumed as stream water entered the streambed in both study sites. The amount of DO uptake was not calculated in the Rouge T2 site because the fractions of stream water in the streambed were not known. However, despite the greater than –0.8 $m \cdot m^{-1}$ VHG in the downwelling zone, DO concentrations declined from 9.0 $mg \cdot L^{-1}$ stream water to 3.2 $mg \cdot L^{-1}$ within a 0.1 m depth (Fig. 7*a*).

Stream water had higher NO_3-N concentrations than in the hyporheic zone in Silver Creek and is a major source of nitrate to the streambed. However, observed subsurface NO_3-N concentrations were consistently lower than the predicted values, assuming NO_3-N was transported identically to Cl^-. Using the mean stream water and groundwater NO_3-N concentrations of 1.34 $mg \cdot L^{-1}$ and 0.30 $mg \cdot L^{-1}$ in the constructed riffle and 1.15 $mg \cdot L^{-1}$ and <0.01 $mg \cdot L^{-1}$ in the natural riffle for baseflow in 2003, sediment depths with >40% stream water should have predicted NO_3-N concentrations of >0.69 $mg \cdot L^{-1}$ and >0.47 $mg \cdot L^{-1}$ in the constructed and natural riffles in Silver Creek, respectively. Observed NO_3-N concentrations in a large portion of the zone of >40% stream water were much lower than these predicted concentrations (Figs. 1 and 4), indicating considerable removal of NO_3-N in the hyporheic zone. The percentage of nitrate removal calculated by comparing observed and predicted NO_3-N concentrations in the constructed riffle often ranged from 50% to 99% (Fig. 8). Removal rates of <50% were observed only within the zone of the >75% stream water fraction, particularly at nest 5 (Figs. 1 and 8). The removal rate in the natural riffle ranged from 41% to 100%, and <50% removal rates were observed only at shallow

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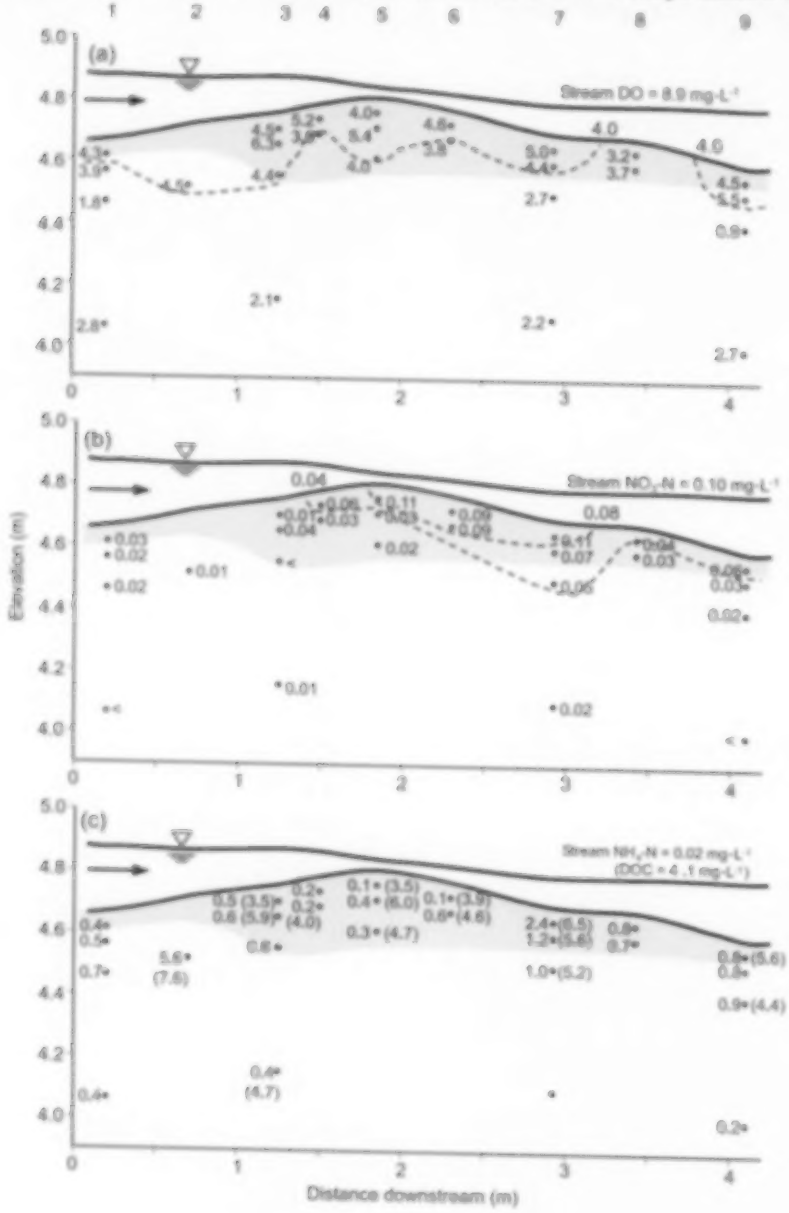
Fig. 6. Rouge T1 site: (*a*) dissolved oxygen (DO) concentration (mg·L^{-1}) on 24 June 2003; (*b*) mean NO_3-N concentration (mg·L^{-1}) during baseflow in May–October 2003; (*c*) NH_4-N concentration (mg·L^{-1}) on 6 October 2003. "<" indicates <0.1 mg·L^{-1}. Shaded area indicates the zone with >10% stream water. DOC, dissolved organic carbon. The underlined triangle indicates the water table.



depths at nests 6 and 7, which did not coincide with the zone of high stream water fraction.

In Rouge tributary sites, co-injection of NaBr and KNO_3 was used to examine nitrate removal. In the Rouge T1 site, the NO_3-N concentration of stream water during the experiment was raised from 0.1 mg·L^{-1} to 0.2 mg·L^{-1}, a value similar to the concentrations observed in spring 2002. Thus, the elevated nitrate concentration during the experiment was within the range of natural fluctuations. If nitrate is transported identically to a conservative ion (Br^-), then nitrate concentrations can be estimated from the fraction of stream water calculated from a two-component mixing equation based on the plateau Br^- concentrations, which were reached by 6.5 h at various sediment depths. The observed nitrate concentrations were always smaller than the calculated concentrations, indicating removal of the stream nitrate in the

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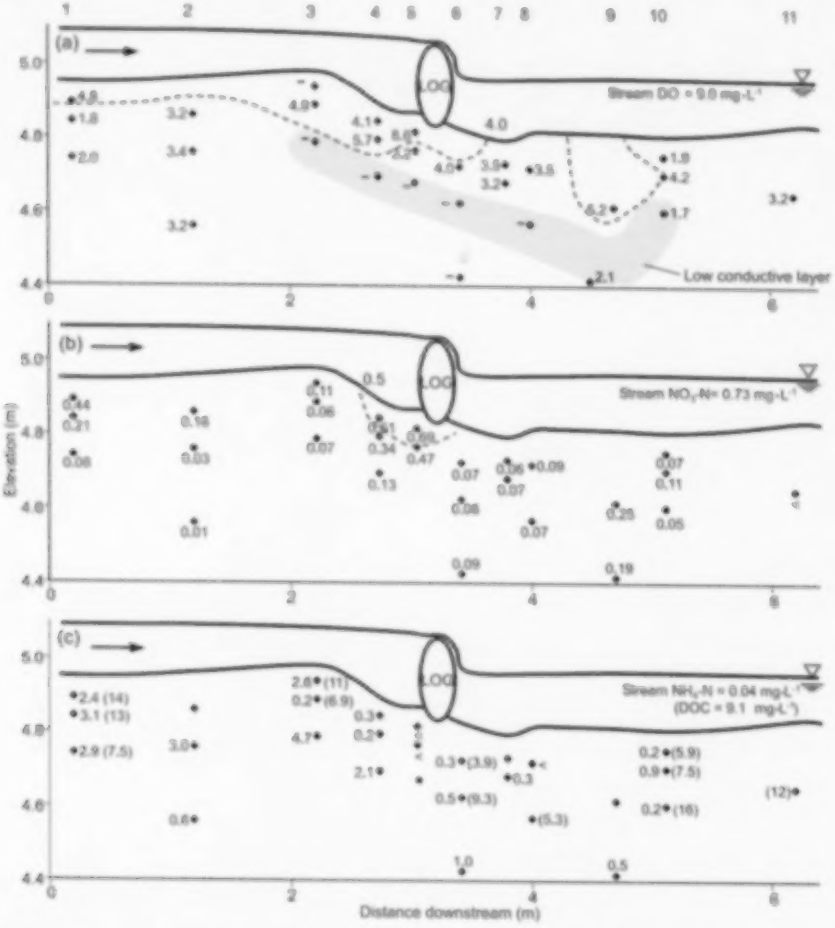
Fig. 7. Rouge T2 site: (*a*) dissolved oxygen (DO) concentration (mg·L^{-1}) on 24 June 2003; (*b*) mean NO_3-N concentration (mg·L^{-1}) during baseflow in May–October 2003; (*c*) NH_4-N concentration (mg·L^{-1}) on 23 October 2003. "<" indicates <0.1 mg·L^{-1}; "–" indicates no measurement. Numbers above represent piezometer nest locations. DOC, dissolved organic carbon. The underlined triangle indicates the water table.



hyporheic zone. The percentage of removal ranged from 22% to 100%, with lower removal rates of <50% being found in the zone of the >75% stream water fraction (Fig. 9*a*).

In the Rouge T2 site, NaBr and KNO_3 were co-injected in a solid state in the streambed. Observed nitrate concentrations in most piezometers were less than the concentrations predicted from the initial ratio of NO_3-N and Br^- mass injected, suggesting nitrate removal. There were no vertical or longitudinal trends in the removal rate (Fig. 9*b*). The removal rate of the piezometers at 0.05–0.1 m depth in nest 4 was low (<10%) at 72 h. However at 24 h, the nitrate removal rate in this zone was ≥50%, and the difference between the observed and predicted NO_3-N concentrations was 25 mg·L^{-1}. The nitrate removal rate then declined progressively at 48 and 72 h, suggesting that the relatively low removal near the injection points at the end of the experiment was the result of temporary saturation of the removal process due to the large concentrations of injected NO_3-N.

The amount of nitrate removed by the hyporheic exchange flow was estimated by multiplying the average percentage of nitrate removal in the hyporheic zone and the fluxes of hyporheic exchange flow estimated using a groundwater flow model, MODFLOW (Kasahara and Hill 2006). The overall amount of nitrate removed by the constructed riffles and step ranged from 0.05 g·day^{-1} in the Rouge Tributary sites to 1.3 g·day^{-1} in the Silver Creek site (Table 2). Although the percentage of nitrate removal was greater in the Silver Creek natural riffle than in the constructed riffle, the amount of nitrate removed was three times greater in the constructed riffle because of the larger hyporheic exchange flux. The fractions of nitrate removed by the constructed features studied were only 0.06%, 0.003%, and 0.003% of the daily stream load in the Rouge T1, Rouge T2, and Silver Creek sites, respectively.

The amount of nitrate removal was also calculated for the zones of higher stream water flux, just downstream from the constructed riffle crest, using the mean percentage of nitrate removal and the fluxes of hyporheic exchange flow occurring in these zones of 544 L·day^{-1} and 950 L·day^{-1}, respectively, in the Rouge T1 and Silver Creek sites (Kasahara and

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Fig. 8. Nitrate-N removal rate (%) calculated from background concentrations of chloride and NO_3-N measured in July–October 2003 at (*a*) the constructed riffle and (*b*) the natural riffle in Silver Creek. "<" indicates <10%. Shaded area indicates the zone with >10% stream water. Numbers above represent piezometer nest locations. The underlined triangle indicates the water table.

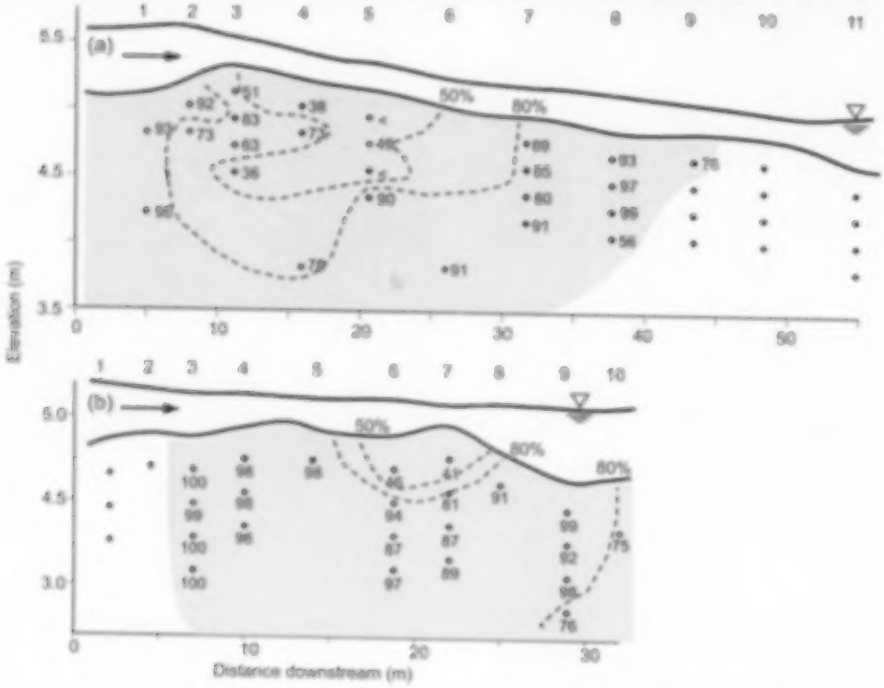
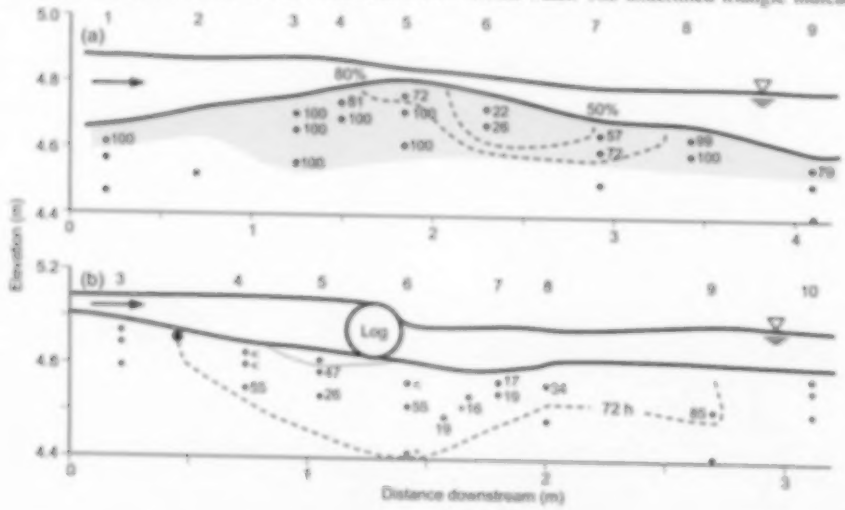


Fig. 9. Nitrate-N removal rate (%) in (*a*) Rouge T1 site calculated from plateau tracer concentrations at 6.5 h into the solute injection and (*b*) Rouge T2 site calculated from the tracer concentrations at 72 h into the experiment. Broken lines indicate the extent of Br^- after 72 h. "<" indicates <10%. Shaded area indicates the zone with >10% stream water. The underlined triangle indicates the water table.



Hill 2006). The nitrate removal estimated in these high stream fraction zones was 0.05 g·day^{-1} and 0.84 g·day^{-1} in the Rouge T1 and Silver Creek sites, respectively. These zones accounted for a large portion of the total amount of nitrate removed by hyporheic exchange flow induced by the riffle (Table 2).

Discussion

The constructed riffles and step induced hyporheic exchange with a clear downwelling–upwelling trend. Zones of intensive hyporheic exchange were located downstream from the riffle crests in the Silver Creek and Rouge T1 sites and

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Table 2. Flux of hyporheic exchange flow (Q_{HEF}) estimated for each study site using MODFLOW simulations and estimated nitrate removal (Kasahara and Hill 2006).

	Rouge T1	Rouge T2	Silver Creek	
			Constructed	Natural
Q_{HEF} (L·day^{-1})	655	91	1356	342
Nitrate removal rate (%)	82	29	69	90
Amount of nitrate removed (g·day^{-1})	0.06	0.02	1.25	0.41

just upstream of the step in the Rouge T2 site. Thus, channel restoration projects that involve construction of riffles and steps contribute to an increase in hyporheic exchange in previously channelized stream reaches.

In the Silver Creek site, the hyporheic zone, identified as the zone with >10% stream water, was extensive in both the constructed and natural riffles, although both riffles had localized groundwater upwelling. The zone with a high stream water fraction was more extensive in the constructed riffle, indicating a greater flux of hyporheic exchange induced by the constructed riffle than by the natural riffle. Several factors may have contributed to this difference. First, the constructed riffle had a steeper longitudinal hydraulic head gradient than the natural riffle, and more hyporheic exchange occurs when the deviation of the riffle head gradient from the average channel gradient is larger (Storey et al. 2003*b*). Second, large cobbles and boulders were added to the streambed surface to construct the riffle, which increased the saturated hydraulic conductivity at a shallow depth in comparison to the natural riffle (Kasahara and Hill 2006). A higher streambed sediment hydraulic conductivity also increases the amount of hyporheic exchange (Morrice et al. 1997). Finally, the upwelling of groundwater was stronger and restricted stream water downwelling significantly in the natural riffle.

A rapid decline of DO concentrations as stream water penetrated into the streambed was apparent, and a large portion of the hyporheic zone remained relatively anaerobic at all study sites. The differences between observed and predicted DO concentrations in the shallow streambed were large, ranging from 1.5 to 4.1 mg·L^{-1} at a 0.05 m depth in the downwelling zone of the Rouge T1 site and from 3.9 to 7.8 mg·L^{-1} at a 0.2 m depth in Silver Creek. These depletion rates of DO are similar to values estimated in the hyporheic zone beneath natural riffle–pool sequences in Brougham Creek, an N-rich cobble–gravel bed stream near Toronto, Ontario (Hill et al. 1998). The rapid decline of DO at a shallow depth in the streambed in these study sites was not expected because the riffles were constructed using cobbles and boulders. Coarse sediments, such as boulders and cobbles, have high hydraulic conductivity, which results in a short contact time between water and sediments, and we hypothesized that the decline of DO level in these coarse substrates should be gradual.

Clogging of the streambed by fine inorganic and organic sediments reduces the saturated hydraulic conductivity of streambeds (Schälchli 1992) and subsequently hyporheic exchange (Weigelhofer and Waringer 2000; Lefebvre et al. 2004). The reduction of saturated hydraulic conductivity increases contact time between water and sediments and results in a hyporheic zone with lower DO concentrations (Findlay 1995). Agricultural and urban landscapes can be a major source of increased silt and fine sediment loads that clog streambed interstitial spaces (Boulton et al. 1997; Hancock 2002). Effluent discharges in urban environments and elevated nutrient fluxes from fertilized cropland can increase stream eutrophication and encourage the growth of dense algal mats and microbial biofilms that create siltation and clogging (Paul and Meyer 2001). Both Silver Creek and the Rouge River tributaries are surrounded by agricultural areas and rapidly expanding urban development. In Silver Creek, average suspended sediment concentrations were 5 mg·L^{-1}, but concentrations increased to maximum values of 139 mg·L^{-1} in high flow periods (Ontario Ministry of Environment). Spring runoff in March and April transports >50% of the annual suspended sediment load in southern Ontario streams (Dickinson et al. 1975). Zones of low saturated hydraulic conductivity (<0.1 m·day^{-1}) were present, and water samples collected from piezometers always had high turbidity, suggesting the occurrence of fine sediments in the boulder layer. In the Rouge T1 site, a silt accumulation was observed at the pool–riffle transition zone, and sandy sediments filled the pore spaces between cobbles in the rest of the reach. Thus, although streambed clogging was not directly measured, these data suggest that clogging was occurring in the study reaches.

Restoration projects designed to rehabilitate degraded streams are usually implemented in streams draining agricultural and urban landscapes and are usually designed to increase surface heterogeneity of stream channels for commercial fish species and stream macroinvertebrates (Kondolf 1995). The primary control on the extent of the hyporheic habitat suitable for macroinvertebrates is the availability of oxygen (Smock et al. 1992; Williams 1993), and DO levels have a significant correlation with hyporheic faunal distribution (Franken et al. 2001). Clogging of the streambed that prevents the downwelling of oxygen-rich stream water creates an unfavorable hyporheic habitat for macroinvertebrates (Boulton et al. 1997). Thus, the addition of coarse substrates in restoration projects may initially increase stream–subsurface water interaction and expand the extent of a relatively aerobic hyporheic zone. However, progressive clogging of these sediments may occur, resulting in a decrease in the aerobic hyporheic zone over time. Thus, control of sediment sources within the watershed may be a key to implementing successful restoration projects that enhance and maintain long-term surface–subsurface linkages.

A trend of decreasing NO_3-N concentration with depth was consistently observed in the hyporheic zone created by the constructed riffles and step studied. The NO_3-N concentrations in the hyporheic zone declined to <40% of the stream water concentrations within depths of 0.2 m and

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0.1 m in the Silver Creek and Rouge Tributary sites, respectively, except for the zone downstream from the riffle crests where the stream water fraction was high and where a more gradual decline of NO_3-N was observed. In contrast to the constructed riffle, NO_3-N concentrations in the Silver Creek natural riffle showed a rapid decline with depth even in the zone of high stream water fraction. These results support the hypothesis that constructed riffles create a more extensive zone of high NO_3-N concentrations.

Differences in observed and predicted streambed NO_3-N concentrations, calculated based on background chloride patterns, showed that nitrate removal occurred in the Silver Creek constructed and natural riffles. The removal of nitrate at Rouge T1 and T2 sites was confirmed by the loss of nitrate in relation to co-injected bromide. Thus, the hyporheic zones in these restored sites function as nitrate sinks, a pattern that is consistent with the conceptual model developed by Jones and Holmes (1996), which suggests that the hyporheic zone is a sink in N-rich streams. Other studies have also reported that the hyporheic zone in natural riffles functions as a nitrate sink in N-rich streams (Hill et al. 1998; Lefebvre et al. 2004).

In Silver Creek and Rouge T1, hyporheic exchange occurring in the zone downstream from the riffle crest in the constructed riffles, where >75% stream water fraction was observed, was dominated by vertical flow and travelled shallow and short distances before returning to the channel and consequently had a large flux and a short residence time (Kasahara and Hill 2006). These characteristics of hyporheic exchange flow may have lowered the percentage of removal in this zone compared with the rest of the hyporheic zone.

Despite the low percentage of nitrate removal, the zones downstream from the riffle crest were estimated to account for a large portion of the total nitrate removed by hyporheic exchange flow induced by the constructed riffles. A large flux occurring in these areas outweighed the effects of a low percentage of nitrate removal. Constructed riffles usually have a steeper longitudinal hydraulic head gradient and a coarser substrate than natural riffles. Although it is likely to be a short time effect if surface clogging occurs, these characteristics of constructed riffles may enhance hyporheic exchange, and constructed riffles may contribute more to nitrate removal in N-rich streams than natural riffles. However, the overall amount of nitrate removed by the constructed riffles and step was a small fraction of the daily load of nitrate in the streams, and many riffles or steps would need to be constructed to create a significant reduction in the nitrate load of stream water in these study reaches.

The processes responsible for nitrate removal were not examined in this study. However, the chemistry patterns in the hyporheic zone suggest that uptake by the biofilm on streambed surface and denitrification, the microbial conversion of nitrate to gaseous forms of nitrogen, may be the primary process of nitrate depletion. Previous studies in N-rich lowland streams have measured high rates of denitrification in stream sediments (Hill and Sanmugadas 1985; Christensen et al. 1989; Lefebvre et al. 2004). Denitrifying bacteria are facultative anaerobes, and their activities are controlled by the availability of oxygen, nitrate, and organic carbon (Korom 1992). In all three study sites, DO concentrations rapidly declined with depth along with NO_3-N concentrations in the hyporheic zone, suggesting that aerobic microbial respiratory processes followed by denitrification occurred at a shallow depth. Low DO values of ≤2.0 mg·L^{-1} were widespread in the Silver Creek sediments. In zones of the Rouge T1 and T2 hyporheic zones where DO concentrations were ≥2.0 mg·L^{-1}, denitrification may still occur in anoxic microsites (Holmes et al. 1996). Patterns of streambed DOC concentrations that were generally >2.0 mg·L^{-1} and were 5–7.5 mg·L^{-1} in some piezometers suggest that carbon was available in the hyporheic zone for denitrifying bacteria.

In summary, hyporheic exchange has been neglected in stream restoration efforts, despite the recognized importance of surface–subsurface linkage in stream ecosystem functions. We expected that the use of cobbles and boulders in the constructed riffles would increase saturated hydraulic conductivity and expand the aerobic hyporheic zone. However, the hyporheic zones created remained relatively anaerobic and functioned as nitrate sinks in the restored sites studied. The coarse substrate used for riffle construction may result in a temporary aerobic hyporheic zone, but its effect can diminish over time. Restoration projects usually focus on degraded agricultural and urban streams, where clogging of the streambed is widespread. Our data suggest that stream restoration projects may have limited long-term effects with respect to increased streambed DO concentrations and associated enhancement of hyporheic fauna habitat unless watershed land use patterns minimize sediment and nutrient runoff to streams.

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Does the river continuum concept apply on a tropical island? Longitudinal variation in a Puerto Rican stream

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Abstract: We examined whether a tropical stream in Puerto Rico matched predictions of the river continuum concept (RCC) for macroinvertebrate functional feeding groups (FFGs). Sampling sites for macroinvertebrates, basal resources, and fishes ranged from headwaters to within 2.5 km of the fourth-order estuary. In a comparison with a model temperate system in which RCC predictions generally held, we used catchment area as a measure of stream size to examine truncated RCC predictions (i.e., cut off to correspond to the largest stream size sampled in Puerto Rico). Despite dominance of generalist freshwater shrimps, which use more than one feeding mode, RCC predictions held for scrapers, shredders, and predators. Collector–filterers showed a trend opposite to that predicted by the RCC, but patterns in basal resources suggest that this is consistent with the central RCC theme: longitudinal distributions of FFGs follow longitudinal patterns in basal resources. Alternatively, the filterer pattern may be explained by fish predation affecting distributions of filter-feeding shrimp. Our results indicate that the RCC generally applies to running waters on tropical islands. However, additional theoretical and field studies across a broad array of stream types should examine whether the RCC needs to be refined to reflect the potential influence of top-down trophic controls on FFG distributions.

Résumé : Nous examinons si un cours d'eau tropical à Porto Rico s'accorde aux prédictions du concept du continuum fluvial (« river continuum concept (RCC) ») en ce qui a trait aux groupes alimentaires fonctionnels (FFG) de macroinvertébrés. Les points d'échantillonnage des invertébrés, des ressources de base et des poissons s'échelonnent des eaux de tête du bassin jusqu'à 2,5 km de l'estuaire, un cours de quatrième ordre. Lors de notre comparaison avec un système modèle des régions tempérées dans lequel les prédictions du RCC se réalisent généralement bien, nous utilisons la surface du bassin versant comme mesure de la taille du cours d'eau afin d'évaluer les prédictions du RCC tronqué (c'est-à-dire amputé de manière à correspondre à la taille maximale de rivière échantillonnée à Porto Rico). Malgré la dominance des crevettes d'eau douce généralistes, qui utilisent plus d'un mode alimentaire, les prédictions du RCC s'appliquent aux racleurs, aux déchiqueteurs et aux prédateurs. Les collecteurs–filtreurs affichent une tendance inverse à celle prédite par le RCC, mais la répartition des ressources de base indique que cela est compatible avec le thème central du RCC qui veut que la répartition longitudinale des FFG suive les patrons longitudinaux des ressources de base. La répartition des filtreurs pourrait aussi s'expliquer par la prédation par les poissons qui affecte les répartitions des crevettes qui se nourrissent par filtration. Nos résultats indiquent que le RCC s'applique généralement bien aux eaux courantes des îles tropicales. Il faudra, cependant, des études théoriques et des travaux de terrain dans une gamme élargie de types de cours d'eau afin de savoir si le RCC doit être raffiné de manière à refléter l'influence potentielle des contrôles trophiques descendants sur les répartitions des FFG.

[Traduit par la Rédaction]

Introduction

Research on tropical streams and rivers has been critical to the development of stream ecosystem theory (sensu Minshall 1988). For example, Junk et al. (1989) based much of the flood-pulse concept on undisturbed conditions of the Amazon River. Tropical stream ecology can also contribute to clarification and refinement of the river continuum concept (RCC); for example, features of tropical streams and rivers have been used to make key points in several theoretical RCC papers (e.g., Minshall et al. 1985; Statzner and Higler 1985). The RCC (Vannote et al. 1980) is a widely used model for interpreting longitudinal patterns in lotic food webs. The concept examines longitudinal changes in the relative importance of autochthonous and allochthonous basal resources, as well as distributions of macroinvertebrate functional feeding groups (FFGs). For example, the RCC predicts that in forested regions, the proportion of total macroinvertebrate biomass attributable to shredders decreases downstream because of a decline in availability of coarse particulate organic matter.

Despite its wide use, the global applicability and utility of the RCC is uncertain because the development of RCC predictions was largely based on river systems draining forested basins of high relief in North America where river–floodplain connections are severely disrupted by hu-

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man activities (e.g., Winterbourn et al. 1981; Minshall et al. 1985; Junk et al. 1989). Alternatively, the RCC may simply need to be further refined and developed to reflect the diversity of river systems in different biomes (Minshall et al. 1985, 1992; de la Rosa 1995). Very little RCC-related or other longitudinal work has been done in the tropics. Tropical data on longitudinal patterns and FFGs are rare (Nair et al. 1989; Dudgeon and Bretschko 1996; Melo and Froehlich 2001). The data that do exist are inadequate for testing the RCC because they (*i*) are based on FFG abundances not biomass, (*ii*) are from a single habitat type such as riffles, and (*iii*) exclude decapod macroinvertebrates and (or) are from highly impacted systems. Whether the RCC is viewed as a narrow construct of temperate North American research or as a broadly useful but not yet fully refined concept for understanding longitudinal biotic patterns, it is clear that more tropical systems need to be examined for comparison to the RCC and its specific predictions.

Tropical island streams and rivers have several unique characteristics that may affect whether they conform to RCC predictions. First, tropical island drainages are often short, entering the ocean as low- or mid-order streams (Smith et al. 2003). As in other regions dominated by small streams that flow directly into oceans (Petersen et al. 1995; Dodds 2002), longitudinal patterns on tropical islands could differ from RCC predictions by being truncated. Second, lotic assemblages of macroinvertebrates on tropical islands are generally dominated by diadromous freshwater shrimps, fishes, and snails (Smith et al. 2003). Because diadromous organisms require a migration between freshwater and salt water to complete their life cycles, waterfalls, which are also common on tropical islands, can cause dramatic longitudinal variation in faunal abundances. Additional characteristics often observed in all types of tropical river systems are poor retention of organic matter because of frequent and unpredictable flash floods (Covich and McDowell 1996; Smith et al. 2003) and an abundance of leaves of poor food quality (e.g., with high concentrations of secondary compounds; Stout 1989). Poor retention and quality of organic matter are thought to cause nonconformance to classic RCC predictions (Winterbourn et al. 1981).

In this study, we describe longitudinal variation in benthic community structure of a tropical stream draining the Luquillo Experimental Forest / Caribbean National Forest (LEF/CNF) on the island of Puerto Rico. Our main objective was to examine whether longitudinal patterns in biomass of macroinvertebrate FFGs follow RCC predictions. We also examined longitudinal patterns in presence or absence of predatory fishes, abundance of algivorous fishes, and standing stocks of algal biomass (chlorophyll *a*), coarse and fine benthic organic matter, and fine benthic inorganic matter. Based on previous qualitative observations of freshwater shrimp and predatory fish distributions in relation to LEF waterfalls (e.g., above waterfall barriers to predatory fish migration, shrimps are at extremely high abundances), we hypothesized that collector–filterers, scrapers, and predators would not conform to classic RCC predictions, whether truncated or not. We reasoned that high abundances of shrimps above waterfalls should result in skewed patterns of macroinvertebrate FFGs because shrimps feed by filtering, gathering, scraping, and predation.

Materials and methods

Study area

The study was conducted at nine sites along a continuous, 13 km stream from its headwaters in an unnamed tributary of Río de la Mina to within 2.5 km of the Río Mameyes estuary (Fig. 1). Río Mameyes enters the ocean as a fourth-order stream, and at mid- and high elevations, the drainage basin contains numerous small and large waterfalls. The five upstream study sites occur in the LEF. The Río Mameyes drainage within the LEF includes the largest tracts of undisturbed primary forest left in the Caribbean (Weaver 1994). The remainder of the drainage occurring within LEF borders is dominated by forest affected by past human activity (i.e., secondary forest that has regrown after agricultural activity early in the 20th century and forest affected by selective harvest; Foster et al. 1999; Clark and Wilcock 2000). The lower four sites occur in surrounding lowlands dominated by secondary forest, pasture and residential areas, and a predominantly forested riparian zone. Río Mameyes is the only river system draining the LEF with no dam on its main stem; however, the lowest elevation site is located at a municipal water intake, which was designed to minimize impact and appears to have no major physical, chemical, or biotic effect on the stream (March et al. 2003). The study region shows only slight seasonal variation in rainfall and allochthonous inputs (Reagan and Waide 1996; Larsen 2000). Unpredictable flash flood events, in which discharge increases up to 10-fold in less than 1 h, occur throughout the year (Covich and McDowell 1996).

Study sites were categorized as being either high elevation and high gradient or low elevation and low gradient (Table 1). High-elevation – high-gradient sites occur above a waterfall or gradient break. High gradients block upstream migration by fishes that prey on freshwater shrimps; however, shrimps can climb waterfalls and maintain large abundances upstream (Covich 1988*a*). Low-elevation sites have lower gradients, and predatory fishes are present. In terms of abundance and biomass, macroinvertebrate assemblages in Puerto Rico are dominated by snails (native Neritinidae and exotic *Thiara granifera*) and three families of migratory shrimps (Xiphocarididae (*Xiphocaris elongata*), Atyidae (*Atya lanipes*, *A. innocous*, *A. scabra*, and *Micratya poeyi*), and Palaemonidae (*Macrobrachium carcinus*, *M. crenulatum*, *M. heterochirus*, *M. faustinum*, and *M. acanthurus*)) (Covich and McDowell 1996). Atyid shrimps often dominate macroinvertebrate communities of headwater streams in Puerto Rico (Pringle 1996), but in mid- to low-elevation streams below waterfalls, adult atyids occur only at low densities (Covich and McDowell 1996). Neritinid and thiarid snails are similarly known to vary in abundance with elevation: they are at high densities in mid- and low-elevation sites and absent at higher elevations (March et al. 2002; Pyron and Covich 2003).

Freshwater shrimps in Puerto Rico have been found to have dramatic effects on algal biomass and species composition, quantity and quality of benthic organic matter, quantity

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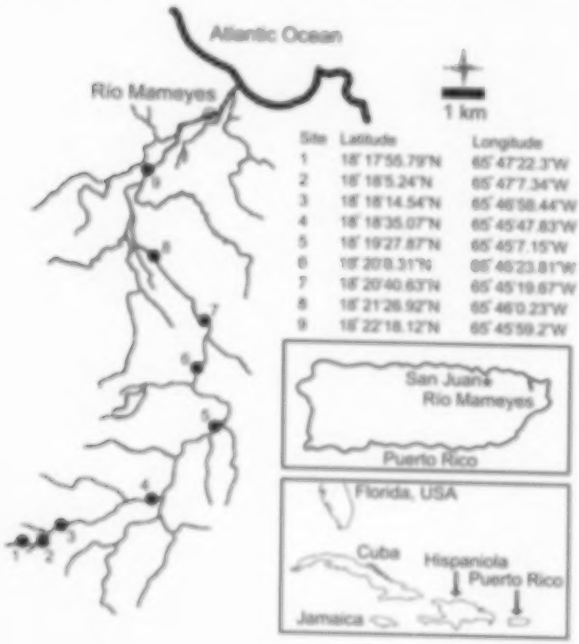
Fig. 1. The Río Mameyes drainage (●, study sites). The upper inset shows the location of the study drainage in Puerto Rico in relation to the capital city, San Juan. The lower inset shows the location of Puerto Rico in relation to Florida, USA, and other islands of the Greater Antilles. Latitude and longitude coordinates of sites are listed (also see Table 1 for site numbers).



of epilithic fine sediments, leaf decomposition rates, and abundance and biomass of benthic invertebrates (e.g., Pringle et al. 1999; Crowl et al. 2001; March et al. 2002). *Sicydium plumieri*, the algivorous green stream goby, is the only fish species that occurs above waterfalls in LEF streams. In Costa Rica, algivorous gobies have been found to affect algal biomass, quantity and quality of benthic organic matter, and abundance of benthic insects (Barbee 2002). Predatory fishes in the Río Mameyes catchment (*Agonostomus monticola*, *Gobiomorus dormitor*, *Eleotris pisonis*, *Awaous tajasica*, and *Anguilla rostrata*) feed primarily on shrimps and other invertebrates (Nieves 1998). Except for the catadromous American eel (*A. rostrata*) and a diadromous eleotrid capable of forming landlocked populations (*G. dormitor*), all native freshwater shrimps, neritinid snails, and fishes in Puerto Rico are thought to be amphidromous, with adult females releasing larvae that passively drift downstream to the estuary before migrating back upstream as juveniles (March et al. 1998; Nieves 1998; Bacheler et al. 2004). Other aquatic fauna of the Río Mameyes catchment are aquatic insects dominated by Baetidae, Leptophlebiidae, Chironomidae, Elmidae, Hydroptilidae, and Simuliidae, benthic invertebrates including Oligochaeta, Copepoda, and Acari, and the crab *Epilobocera sinuatifrons* (Covich and McDowell 1996; Zimmerman and Covich 2003).

Methods

At each site, we established a reach that was 10 times the channel width and visually identified major habitats (Table 1). Proportional availability of major habitats was determined using occurrence frequency of mesohabitats (riffles, pools, and runs, based on measured lengths) combined with occurrence frequency of substrates (based on 54 random measurements in each major mesohabitat type). All measurements and samples were taken during base flow from June through August 2001. Epilithic chlorophyll *a* was sampled using a suction device modified from Loeb (1981). We collected a pooled sample of four individual and randomly located Loeb samples in each of three pools and three riffles at each site. Chlorophyll *a* samples were brought back to the lab on ice, filtered, frozen, and analyzed fluorometrically according to standard methods (American Public Health Association 1985).

To measure non-shrimp benthic invertebrate densities and standing stocks of very fine (VF, <250 µm) and medium fine (MF, 250 µm – 1 mm) benthic inorganic matter (BIM) and VF, MF, and coarse (C, >1 mm) benthic organic matter (BOM), three randomly located samples per major habitat were collected and processed using methods modified from Lugthart and Wallace (1992) and Grubaugh et al. (1996). Macrophytes in runs, as well as sand habitats in pools, were sampled using a core of known area. Pools with boulders and interstitial cobble and gravel were sampled using the "benthic block net" method described by Greathouse and Pringle (2005); the benthic block net apparatus functions similarly to a core. Bedrock–boulder cascades were sampled by scrub-brushing invertebrates and benthic matter from a known area into a hand net or into a Surber sampler with foam rubber tied around the frame to create a seal with the substrate. Cobble–coarse gravel riffles were sampled with an unmodified Surber net. In cobble runs, a sample consisted of a single cobble placed into a downstream D net, scrubbed on the bank to remove invertebrates and benthic matter, and measured to determine surface area. Because hand, Surber, and D nets were 250 µm mesh, we further modified methods of Lugthart and Wallace (1992) and Grubaugh et al. (1996) by using the Loeb sampler to collect VFBOM and VFBIM in Surber and hand-net samples, and we used the Loeb sampler on nearby cobbles to estimate VFBOM and VFBIM in D-net samples. An additional modification is that we did not separate macrophytes from coarse detritus when measuring standing stocks of CBOM; however, macrophytes only occurred in run and riffle samples at the lowest-elevation site (*Hydrilla*) and in a single riffle sample at site 3 (filamentous algae). Invertebrate samples were preserved in the field in ethanol.

Samples intended for estimating VFBOM/BIM (from Loeb, core, and benthic block net sampling) were sieved to remove material >250 µm before filtration onto pre-ashed, pre-weighed glass fiber filters (Whatman GF/F, 0.7 µm). Non-decapod invertebrate samples were separated into MF and C fractions using nested 1 mm and 250 µm sieves before sorting for macroinvertebrates. After sorting, we subsampled the MFBOM/BIM for filtration onto a pre-ashed, pre-weighed glass fiber filter. CBOM and filters of VFBOM/BIM and MFBOM/BIM were dried for 24 h at 50 °C, weighed, ashed for 3 h at 500 °C, and reweighed to determine ash-free dry mass (AFDM) for VFBOM, MFBOM, and CBOM and inorganic dry mass for VFBIM and MFBIM. Non-decapod invertebrates were identified to the lowest practicable level

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Table 1. Study site physical characteristics.

Site	Stream	Stream type[a]	Stream order[b]	Catchment area (ha)	Elevation (m asl)[c]	Slope (%)	Mean width[d] (m)	Canopy cover[e] (%)	Major habitats
1	Unnamed	High	0	4	720	16.8	3.0	89.5	Sand pools, boulder–bedrock riffles
2	Unnamed	High	1	32	660	14.8	4.5	83.2	Boulder pools, cobble riffles
3	Río de la Mina	High	2	136	590	12.7	8.3	43.3	Boulder pools, boulder–bedrock riffles
4	Río de la Mina	High	2	506	250	7.8	11.0	40.3	Boulder pools, boulder–bedrock riffles
5	Río Mameyes	Low	3	1574	105	4.0	21.0	15.5	Boulder pools, boulder–bedrock riffles
6	Río Mameyes	Low	3	2025	65	1.6	14.5	29.7	Boulder pools, boulder–bedrock riffles
7	Río Mameyes	Low	3	2225	42	1.8	16.6	33.9	Boulder pools, boulder–bedrock riffles
8	Río Mameyes	Low	3	2422	16	0.8	15.0	22.2	Boulder pools, cobble riffles
9	Río Mameyes	Low	3	3455	5	0.7	13.0	22.7	Cobble runs, macrophytes,[f] cobble riffles

[a]High, high elevation – high gradient; low, low elevation – low gradient.
[b]Based on blue lines from US Geological Survey 1:20 000 topographic maps. Stream order 0 site is a headwater stream without a blue line.
[c]Units are metres above sea level (m asl).
[d]Bankfull measurements.
[e]Spherical densiometer measurements.
[f]Macrophytes were *Hydrilla* in runs.

(generally family or subfamily for insects and class or order for other non-decapod invertebrates; note that we consider potential bias of FFG designation from this level of identification in the Discussion). Length–mass regressions, determined from individuals preserved in ~10% formaldehyde, were used to determine snail biomass (Appendix A). Published (Benke et al. 1999) and unpublished (W. Cross, Institute of Ecology, University of Georgia, Athens, GA 30602, USA, personal communication) length–mass regressions were used to determine biomass of other non-decapod invertebrates. Functional feeding group designations of non-decapod invertebrates followed those of March (2000) and were based on Buzby (1998) and Merritt and Cummins (1996).

We obtained quantitative estimates of shrimp and crab biomass and fish abundance by electroshocking and snorkeling. A minimum of one pool or run habitat and one riffle habitat per site were electroshocked using depletion or removal sampling methods (White et al. 1982; Fièvet et al. 1996, 1999). Block and dip nets were 0.635 cm mesh. Captured shrimps and crabs were identified to genus or species and measured to the nearest millimetre for postorbital carapace length (Hobbs 1991). Electroshocking was ineffective for capturing gobies (*Sicydium* and *Awaous*) and sleepers (Eleotridae) in pools, as has been observed by other researchers for Puerto Rico (E. García, US Department of Agriculture Forest Service, Southern Region, Atlanta, GA 30309, USA, and N. Hemphill, Trinity County Resource Conservation District, Weaverville, CA 96093, USA, personal communication). Thus, in one pool or run per site, we snorkeled a known area, counting all gobies and sleepers observed. Visibility was similar across sites. Carapace length–mass regression equations for shrimps and crabs, determined from individuals preserved in ~10% formaldehyde, were used to determine shrimp and crab biomass (Appendix A). In determining biomass of macroinvertebrate functional feeding groups, we apportioned biomass of shrimp taxa equivalently to each known functional feeding group membership (Table 2).

Data analysis

For both our analytical approach and our basis for comparison with RCC functional group predictions, we used a model study demonstrating that the RCC generally applies to macroinvertebrate communities along a continuous, 65 km reach from the headwaters of Ball Creek to the Little Tennessee River (via Coweeta Creek) in North Carolina, USA (Grubaugh et al. 1996). The analytical approach consisted of linear regressions of arcsine-transformed percentages of habitat-weighted functional group biomass against catchment area. We also used linear regression against catchment area to analyze other ecosystem and community structure parameters.

To compare results from the Little Tennessee River drainage with results from the Río Mameyes drainage, regression lines from Grubaugh et al. (1996) were included in plots of habitat-weighted biomass of functional groups vs. catchment area and percent functional group biomass vs. catchment area. Although our data are from sampling at only one time of year, whereas regressions from Grubaugh et al. (1996) are based on annual means from seasonal sampling, we consider ours to be reasonable estimates of annual means because

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Table 2. Decapod functional feeding group (FFG) apportionment used for this study.

Taxa	Scraper	Shredder	Gatherer	Filterer	Predator	References for known FFGs
Shrimp						
Xiphocaris elongata	1/3	1/3	1/3	—	—	Fryer 1977; Crowl et al. 2001; March et al. 2001
Atya scabra	—	—	—	1	—	Fryer 1977; Covich 1988*a*
Atya lanipes	1/3	—	1/3	1/3	—	Fryer 1977; Covich 1988*a*
Atya innocous	1/3	—	1/3	1/3	—	Fryer 1977; Covich 1988*a*
Micratya poeyi	1/3	—	1/3	1/3	—	Fryer 1977
Juvenile *Atya* spp.	1/3	—	1/3	1/3	—	(Ambiguous atyids likely *A. lanipes* or *A. innocous*)
Macrobrachium spp.	—	—	1/2	—	1/2	Crowl and Covich 1994; Covich and McDowell 1996; March et al. 2001
Crab						
Epilobocera sinuatifrons	—	—	1/2	—	1/2	Covich and McDowell 1996; Henry 2000

Note: For each taxon, apportionments were split into equivalent proportions for each mode of feeding known from references in the literature. Gatherer, collector–gatherer; filterer, collector–filterer.

intra-annual variation in climate (Ramírez and Melendez-Colom 2003) and standing stocks of algae (C. Pringle, E. Greathouse, K. Smith, unpublished data), organic matter (C. Pringle, E. Greathouse, K. Smith, unpublished data), and macroinvertebrates (Masteller 1993; Covich et al. 2003) in Puerto Rico is inconsistent, with no clear seasonal patterns.

We presupposed that examining whether the Río Mameyes drainage follows RCC predictions requires comparison of our data with RCC predictions cut off at mid-orders. For example, the RCC predicts a hump-shaped pattern for scrapers because of low representation in forested headwaters, maximum importance in mid-orders (~3rd to 5th order), and low representation in high orders (>6th order). But for a stream entering the ocean at 4th order, the proportional representation of scrapers should increase along the entire stream length from headwaters to ocean. Thus, in comparing patterns of percent functional group biomass vs. catchment area, our primary focus was to compare our data with the portion of the regression lines from Grubaugh et al. (1996) that would correspond to truncation at a catchment area of 3500 ha (equivalent to a 3rd-order stream based on blue lines of a US Geological Survey (USGS) 1:25 000 topographic map) to exclude portions of the regression that correspond to sites of much greater size than our sampling sites (i.e., truncation excludes areas where catchment area, order, width, depth, discharge, etc., indicate a stream size much larger than our largest sampling site). However, the figure of percent functional group biomass vs. catchment area shows the full nontruncated regression lines from Grubaugh et al. (1996) to also allow examination of the Río Mameyes pattern in a broader context. The figure of habitat-weighted biomass of functional groups vs. catchment area does not include full nontruncated regression lines from Grubaugh et al. (1996); regression lines from Grubaugh et al. (1996) in this figure were truncated at ~4000 ha because a nonlogarithmic x axis with a maximum value of 4000 ha was necessary to clearly illustrate the patterns in the Río Mameyes data (i.e., extending the x axis to 125 000 ha to correspond to the largest catchment area from Grubaugh et al. (1996) makes the Río Mameyes data too small to see and extending the x axis to 1 000 000 ha and making it logarithmic obscures the patterns in the Río Mameyes data).

Truncation at 3500 ha excludes all portions of the regressions corresponding to sampling sites on the Little Tennessee River. Moreover, regressions in each study are based on data from sites located along our definition of a "continuum": a continuous length of stream that spans several orders (i.e., sites were along a single channel from upstream to downstream). Thus, when describing and discussing the results of our comparison, we use "Río Mameyes continuum", "Coweeta Creek continuum", and "Little Tennessee River continuum" to distinguish between the two drainages and truncated ("Coweeta Creek continuum") and nontruncated ("Little Tennessee River continuum") portions of the Little Tennessee River drainage.

Geomorphic features are broadly comparable between the drainages of the Río Mameyes (outlet at site 9) and Coweeta Creek (outlet at site M-5 from Grubaugh et al. 1996). Both outlets are 3rd order (based on blue lines from USGS topographic maps). The continuums also have similar basin lengths (Coweeta, 9.2 km; Mameyes, 9.8 km), relief ratios (Coweeta, 0.10; Mameyes, 0.10), average stream slopes (Coweeta, 0.05; Mameyes, 0.05), and elongation ratios (Coweeta, 0.8; Mameyes, 0.7; an indicator of basin shape) (see Gordon et al. (1992) for equations used to calculate geomorphic characteristics). Annual runoff is ~2 times higher in the Río Mameyes drainage (~2.6 m) than in the Coweeta drainage (~1.1 m). Similarly, bankfull widths are somewhat higher on average in the Río Mameyes (~12 m) than in the Coweeta drainage (~8 m). In comparing FFG patterns between the Río Mameyes and Coweeta Creek continuums, we decided against using other measures of stream size (or position along the continuum) in our figures because other measures either would have given very similar results (e.g., high correspondence between catchment area and order between the two drainages suggests that results would have been similar if data were plotted against order) or are inadequately characterized in Grubaugh et al. (1996) and (or) the Río

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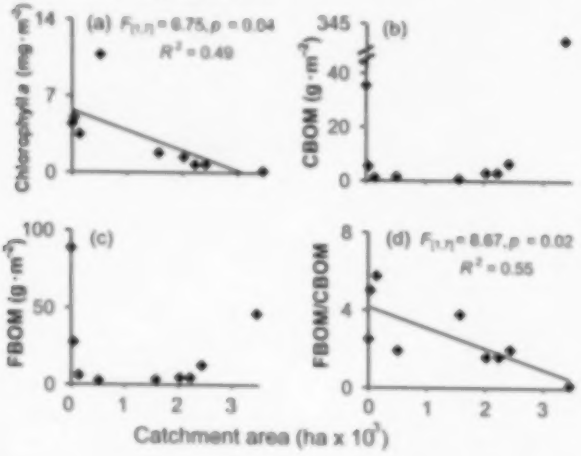
Fig. 2. Patterns in standing stocks of basal resources along the Río Mameyes continuum: (*a*) epilithic chlorophyll *a*, data points are means from three pools and three riffles at each site; (*b*) habitat-weighted coarse (C, >1 mm) benthic organic matter (BOM); (*c*) habitat-weighted fine (F, <1 mm) BOM; (*d*) ratio of F to C habitat-weighted BOM.



Mameyes basin. For example, there are only two gauges along the Río Mameyes continuum, and thus, to compute mean annual runoff or discharge, we would have had to have used a linear regression between catchment area and flow. Grubaugh et al. (1996) also had to use such a regression to estimate mean annual discharge at several of their sites. Thus, if we had plotted figures against runoff, Mameyes data points would simply have been shifted to the right relative to Grubaugh et al. (1996) regression lines.

We used linear regressions among shrimps and ecosystem and community properties (standing stocks of chlorophyll *a*, BOM, BIM, macroinvertebrates) to examine whether there are negative correlations between shrimps and ecosystem and community properties that are consistent with previous shrimp exclusion experiments (e.g., Pringle et al. 1999; March et al. 2002). Because these past shrimp exclusions were conducted in pools, we conducted separate regressions for pools (and runs) and for riffles. We also examined linear regressions between total non-decapod invertebrate biomass and BOM. For simplicity of data presentation, VF and MF size fractions were generally combined into a single "fine" size fraction. For statistical analyses, we used JMP 3.2.6 (SAS Institute Inc. 1999) and a significance level of 0.05. All percentages were arcsine-transformed before statistical analyses. For nonpercentage data, the Shapiro–Wilk test was used to test for normality, and when appropriate, $\log_{10}(x + 1)$ transformations were conducted.

Results

Standing stocks of chlorophyll *a* in periphyton decreased along the Río Mameyes continuum (Fig. 2*a*), as did the ratio of habitat-weighted FBOM to CBOM (Fig. 2*d*). Absolute standing stocks of FBOM and CBOM showed no longitudinal trend but were highest at the extremes of the continuum (Figs. 2*b* and 2*c*). Habitat-weighted atyid shrimp biomass was dramatically higher in high-elevation sites (Fig. 3). In contrast, habitat-weighted biomass of gastropods was dramatically higher at the two lowest-elevation sites, whereas habitat-weighted biomass of other macroinvertebrates was more even across the continuum (Fig. 3). Predatory fishes were not present in electroshocking samples and during snorkeling observations at sites with catchments smaller than approximately 1000 ha (Fig. 3; Appendix B, Table B1). Highest densities of the green stream goby occurred in mid-elevation sites, and no *Sicydium* were found at the highest- and lowest-elevation sites (Table 3). Macroinvertebrate biomass, standing stocks of basal resources, and proportional representation of habitats used in habitat weighting are listed by habitat unit and site (Appendix B, Tables B2–B5).

Fig. 3. Habitat-weighted biomass of atyid decapods (■), gastropods (△), and other macroinvertebrates (● and broken line) along the Río Mameyes continuum. Solid black bar on *x* axis indicates region containing waterfall barrier to upstream migration of predatory fishes. AFDM, ash-free dry mass.

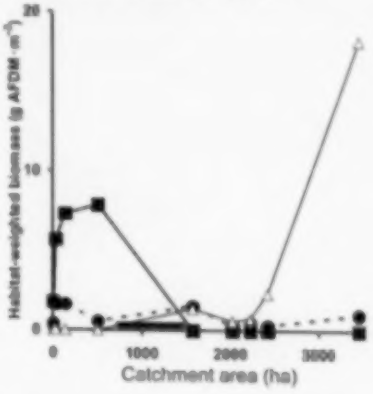


Table 3. Habitat-specific densities of the green stream goby, *Sicydium plumieri*, along the Río Mameyes continuum.

Site	*Sicydium* in pools[a] (no.·m^{-2})	*Sicydium* in riffles[b] (no.·m^{-2})
1	0.00	0.00
2	0.00	0.21
3	2.93	0.44
4	1.65	1.44
5	0.60	0.21
6	0.52	0.20
7	0.50	0.10
8	0.00	0.01
9	0.00	0.00

[a]Snorkeling data.
[b]Electroshocking data.

For habitat-specific analyses, macroinvertebrate functional feeding groups showed variable trends in dominance along the continuum (Fig. 4). Relative dominance of scrapers increased and shredders decreased along the continuum in boulder–bedrock pools, but both functional groups showed no trend in boulder–bedrock riffles. Percentages of collector–gatherers decreased with catchment area in boulder–bedrock pools but increased in boulder–bedrock riffles. Percentages

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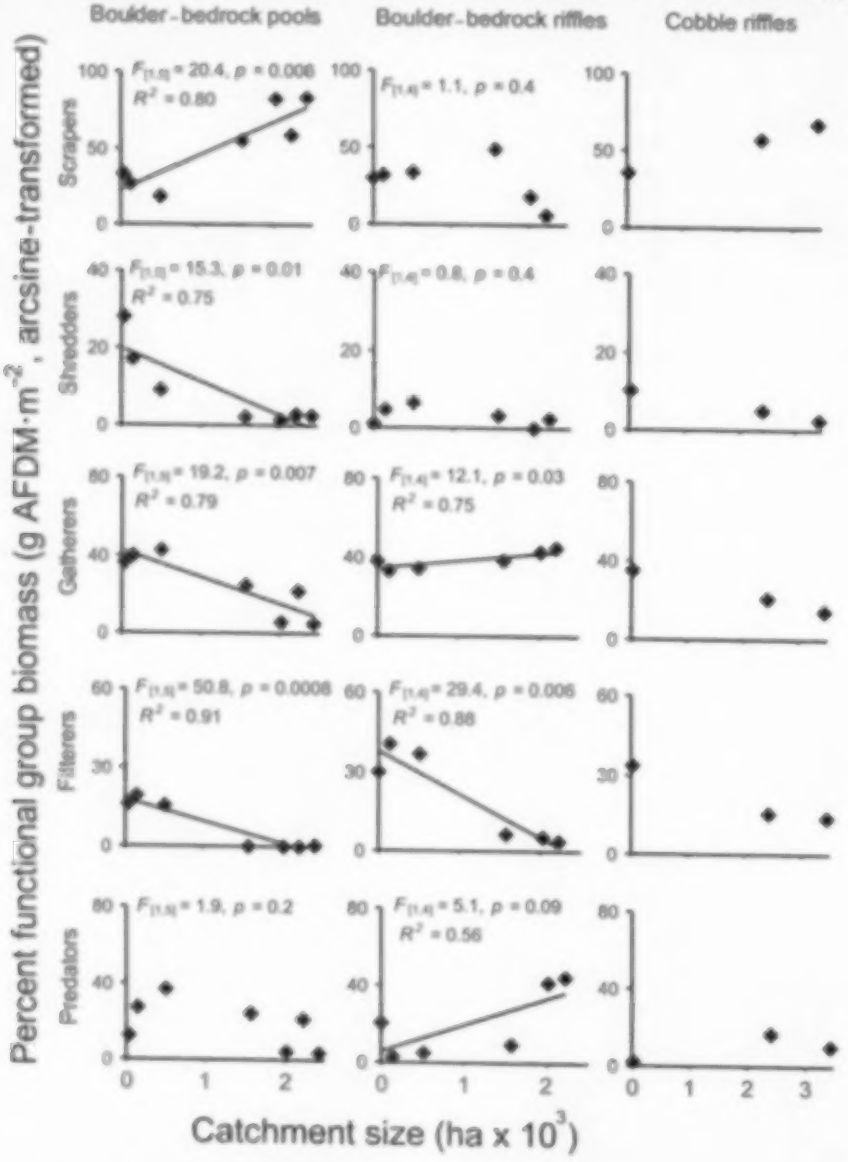
Fig. 4. Relative dominance of macroinvertebrate functional feeding groups in bedrock–boulder pools, bedrock–boulder riffles, and cobble riffles along the Río Mameyes continuum. Data are arcsine-transformed percentages of total habitat-specific biomass at each sampling site. Note that gatherers denotes collector–gatherers and filterers denotes collector–filterers. AFDM, ash-free dry mass.



of collector–filterers in both boulder–bedrock pools and boulder–bedrock riffles decreased with catchment area. Predators showed no trend in boulder–bedrock pools and a marginally significant trend of increasing with stream size in boulder–bedrock riffles. Cobble riffle data are presented but not analyzed for statistical trends because cobble riffles occurred at only three sites (Fig. 4, third column). Cobble–macrophyte runs at the lowest-elevation site were dominated by scrapers (scrapers were 97% of total invertebrate biomass in runs). Sand pools at the highest-elevation site were dominated by collector–gatherers, collector–filterers, and scrapers (33%, 29%, and 32% of total invertebrate biomass, respectively). Total macroinvertebrate biomass was highest in cobble–macrophyte runs at the lowest-elevation site where mean total biomass was 24.9 g AFDM·m^{-2}. Among the three other habitat types, total macroinvertebrate biomass was fairly equivalent (mean total biomass: boulder–bedrock pools, 4.2 g AFDM·m^{-2}; boulder–bedrock riffles, 3.9 g AFDM·m^{-2}; cobble riffles, 5.8 g AFDM·m^{-2}; sand pools at highest-elevation site, 3.3 g AFDM·m^{-2}).

Longitudinal patterns in absolute values of habitat-weighted biomass in the Río Mameyes continuum generally

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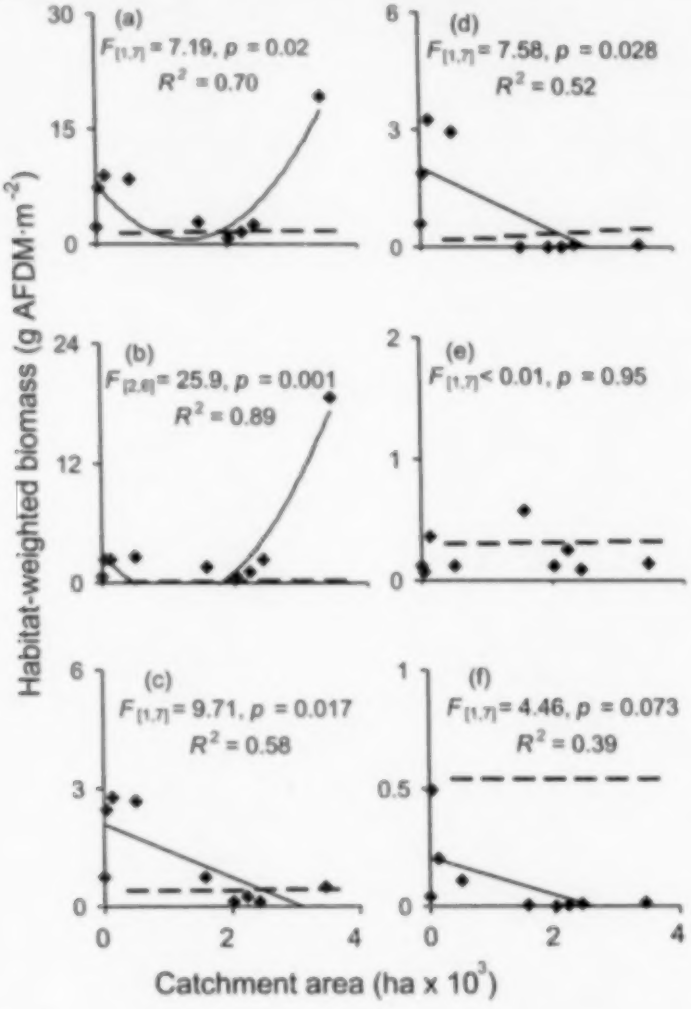
Fig. 5. Habitat-weighted biomass of macroinvertebrate functional feeding groups along the Río Mameyes continuum (◆ and solid regression lines) and the Coweeta Creek continuum (broken regression lines, from Grubaugh et al. 1996; regression lines are truncated at ~4000 ha). Total biomass of (*a*) macroinvertebrates, (*b*) scrapers, (*c*) collector–gatherers, (*d*) collector–filterers, (*e*) predators, and (*f*) shredders. AFDM, ash-free dry mass.



did not match patterns in the Coweeta Creek continuum, which usually showed little to no variation over the spatial scale of comparison (Fig. 5). Predators were the only functional feeding group in the Río Mameyes continuum to closely match the Coweeta Creek pattern. Mean habitat-weighted biomass of predators in the Río Mameyes continuum was 0.2 g AFDM·m^{-2} compared with ~0.3 g AFDM·m^{-2} in the Coweeta Creek continuum (Fig. 5). Total habitat-weighted biomass in the Río Mameyes continuum showed a polynomial trend with catchment area, and the mean across all sites was 6.0 g AFDM·m^{-2}, a much higher value than the ~1.4 g AFDM·m^{-2} in the Coweeta Creek continuum. In the Río Mameyes continuum, a polynomial function fit the pattern for habitat-weighted biomass of scrapers, which reached much higher values compared with the Coweeta Creek regression line (Fig. 5). Habitat-weighted biomass of both collector–gatherers and collector–filterers decreased along the Río Mameyes continuum, from values much above the Coweeta Creek regression at high-elevation sites to values comparable to the Coweeta Creek continuum at low-elevation sites. For shredders, habitat-weighted biomass showed a marginally significant trend of decreasing along the Río Mameyes continuum and was generally much lower than shredder biomass in the Coweeta Creek continuum (Fig. 5).

No regressions between percent functional group biomass and catchment area in the Río Mameyes continuum closely matched regressions in the Coweeta Creek continuum, but the directions of some trends did match (Fig. 6). Along both the Río Mameyes and Coweeta Creek continuums, percent functional group biomass increased for scrapers and decreased for shredders (note that the entire Little Tennessee River

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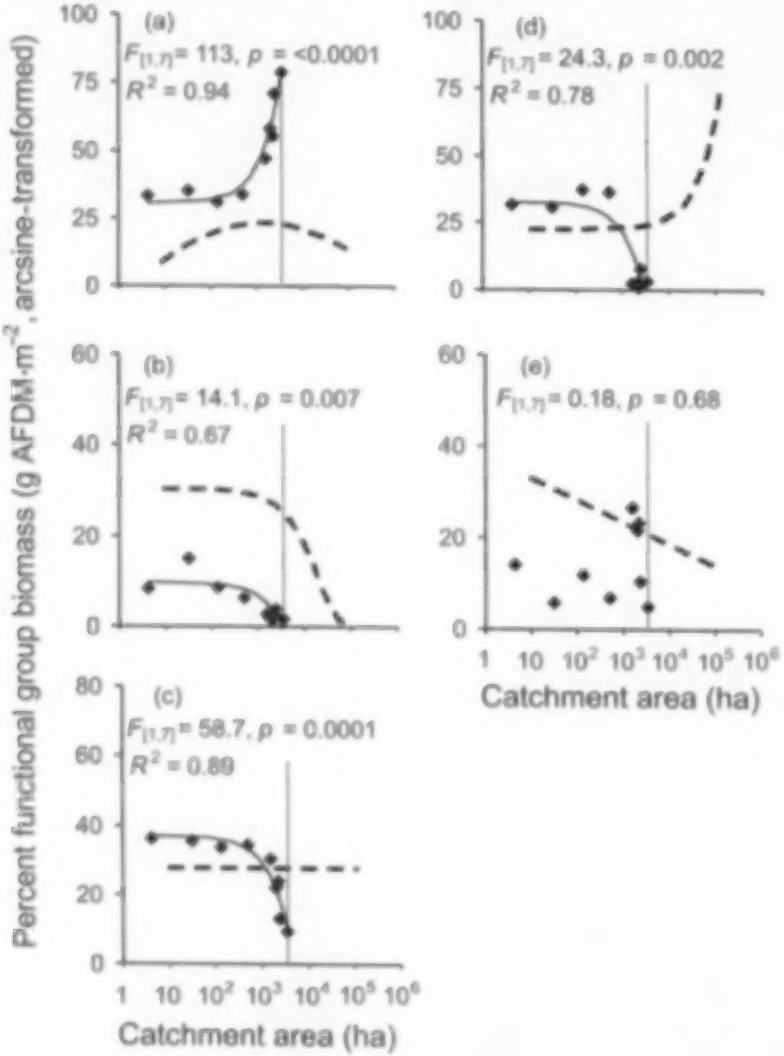
Fig. 6. Relative dominance of macroinvertebrate functional feeding groups along the Río Mameyes continuum (◆ and solid regression lines) and the Little Tennessee River continuum (broken regression lines, from Grubaugh et al. 1996). Vertical lines indicate the catchment area where truncating the Little Tennessee River continuum allows comparison of the Río Mameyes continuum with the Coweeta Creek continuum. Plots are arcsine-transformed percentages of habitat-weighted biomasses at each sampling site: (*a*) scrapers, (*b*) shredders, (*c*) collector–gatherers, (*d*) collector–filterers, and (*e*) predators. Note that significant regression lines for Mameyes data appear curved because of the log scale of the *x* axis. AFDM, ash-free dry mass.



continuum showed a hump-shaped pattern) (Fig. 6; Table 4). Percent contribution of shredders in the Río Mameyes continuum was less than 7% at all sites (Table 4) and was much lower than the percent contribution of shredders in the Coweeta Creek continuum (Fig. 6). Relative dominance of collector–gatherers and collector–filterers decreased along the Río Mameyes continuum, whereas collector–gatherers and collector–filterers showed little to no change along the Coweeta Creek continuum and collector–filterers showed a large increase along the entire Little Tennessee River continuum (Fig. 6; Table 4). Percent contribution of macroinvertebrate predators showed no trend along the Río Mameyes continuum but decreased along the Coweeta Creek continuum (Fig. 6; Table 4).

In pools–runs, the only correlations between any of the shrimp genera and ecosystem properties were marginally significant and positive. In riffles, biomass of atyids and *Xiphocaris* were positively correlated with chlorophyll *a* (atyids, $F_{[1,7]}$ = 23.0, P = 0.002; *Xiphocaris*, $F_{[1,7]}$ = 6.5, P = 0.036). Biomass of riffle atyids was also positively correlated with VFBOM ($F_{[1,7]}$ = 28.8, P = 0.001), and biomass of *Xiphocaris* shrimp was positively correlated with FBOM ($F_{[1,7]}$ = 8.8, P = 0.021) and VFBIM ($F_{[1,7]}$ = 11.8, P = 0.011). Total biomass of non-decapod invertebrates was pos-

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Table 4. Percent of habitat-weighted biomass in each macroinvertebrate functional feeding group at sites along the Río Mameyes continuum.

Site	Scrapers	Shredders	Gatherers	Filterers	Predators
1	29.8	2.0	34.8	27.6	5.8
2	32.7	6.7	33.7	25.9	1.0
3	26.3	2.2	31.0	36.4	4.1
4	30.4	1.3	31.9	35.0	1.4
5	53.9	0.2	25.8	0.2	19.9
6	71.8	0.1	14.3	0.2	13.6
7	67.9	0.2	16.2	<0.1	15.7
8	89.2	0.5	5.0	2.0	3.3
9	96.2	0.1	2.6	0.3	0.7

Note: Gatherers, collector–gatherers; filterers, collector–filterers.

itively correlated with CBOM in pools and runs ($F_{1,7} = 77.6$, $P < 0.0001$). Total biomass of non-decapod invertebrates in riffles showed no correlations with BOM, regardless of size fraction. Chlorophyll *a* was negatively correlated with habitat-weighted biomass of snails ($F_{1,7} = 9.91$, $P = 0.016$). Habitat-weighted biomass of atyid shrimp was also dramatically higher where habitat-weighted snail biomass was zero ($F_{1,7} = 57.81$, $P < 0.0001$). Sampled snail biomass was zero at all high-elevation sites (sites with catchment areas smaller than ~1000 ha); however, we did observe that snails were present during fieldwork at high-elevation site 4.

Discussion

Do macroinvertebrate FFGs match RCC predictions?

Functional groups in the Río Mameyes continuum conform broadly to truncated RCC predictions for some FFGs but not others. Relative contributions of shredders and scrapers clearly fit RCC predictions and match the Coweeta Creek trends (Grubaugh et al. 1996) by decreasing and increasing, respectively, from headwaters to mid-orders. We expected the shredder pattern because the dominant shredder in Puerto Rico, *X. elongata*, is known to have high abundances above waterfalls (March et al. 2001). We did not expect the scraper pattern because we did not anticipate snail biomass at low elevations overwhelming contributions from high densities of shrimp scrapers at high elevations.

Relative contributions of predators, gatherers, and filterers do not match trends in the Coweeta Creek continuum. Predators were the only FFG for which the Coweeta Creek continuum did not conform to the RCC prediction (Grubaugh et al. 1996). Our findings do conform to the RCC prediction that relative contributions of predators do not change with stream size (Vannote et al. 1980). However, we hypothesized that predators would decrease downstream (as observed in the Coweeta Creek continuum), because in both systems, there are downstream increases in densities of predatory fishes, which have the potential to competitively exclude invertebrate predators. For gatherers, it is difficult to make conclusions regarding whether the decrease in relative contributions along the Río Mameyes continuum conforms to the RCC or not because the exact RCC prediction is unclear. Grubaugh et al. (1996) found no change in percent gatherer biomass with stream size. The original RCC (Vannote et al. 1980) did not make a separate and clear prediction for gatherers: gatherers were grouped with filterers in a single collector category, and collector representation was predicted to remain constant from headwaters to mid-orders. In their revision of the RCC, Minshall et al. (1985) characterize gatherers as decreasing slightly from headwaters to mid-orders. Filterers are the one FFG in the Río Mameyes continuum that clearly does not conform to RCC predictions. We found that filterers decrease in relative dominance downstream, but the RCC prediction is that contributions of filterers either do not change substantially (Vannote et al. 1980; Grubaugh et al. 1996) or increase (Minshall et al. 1985) from headwaters to mid-orders. The filterer pattern matches our hypothesis that dominance of atyid shrimps in headwaters would cause a downstream decrease in filterers.

The direction of regression slopes for relative contributions in the Río Mameyes continuum match those of the Coweeta Creek continuum and RCC predictions for several FFGs. However, actual percent representation and standing stocks of FFG biomass are strikingly different from patterns observed by Grubaugh et al. (1996). The Río Mameyes continuum has low representation of shredders, which is thought to be typical of many tropical regions including Asia (Burton and Sivaramakrishnan 1993; Yule 1996*b*; Dudgeon 1999), the Pacific islands (Resh and de Szalay 1995), Africa (Minshall et al. 1985), and the neotropics (Wootton and Oemke 1992; Mathuriau and Chauvet 2002). Shredders appear to be largely replaced by scrapers, gatherers, and filterers.

Our findings do not support the hypothesis that low representation of shredders in tropical streams is an artifact of macroinvertebrate-focused FFG analyses that only consider insect shredders and exclude other biota, such as crustaceans and fishes, that may be important leaf feeders in the tropics (Ramírez and Pringle 1998; Dudgeon and Wu 1999; Moss 2005). We found that shredder biomass is poorly represented despite the fact that we included all potential shredders and leaf feeders (calamoceratid caddisflies, the elmid beetle *Phanocerus* (Buzby 1998), and leaf-mining chironomids (E. Greathouse, personal observation); *X. elongata*; no stream fishes are CPOM detritivores in Puerto Rico).

Ours is the first tropical study to our knowledge that evaluates FFG predictions of the RCC using appropriate methods. Regional reviews of stream ecology have noted the lack of adequate longitudinal and functional group data for tropical Asia (Dudgeon 1999), the Pacific islands (Resh and de Szalay 1995), the Caribbean and Central America (de la Rosa 1995), South America (Lewis et al. 1995), and Africa (Cooper 1996). Valid evaluation of RCC predictions and use of the RCC as a comparative tool require methods of sampling and analysis similar to those used in the development of the RCC (Barmuta and Lake 1982). Tropical FFG data that do exist are from Asia (e.g., Dudgeon 1984; Burton and Sivaramakrishnan 1993), the Pacific islands (Dudgeon 1994; Yule 1996*b*), Africa (Cooper 1996; Tumwesigye et al. 2000), and Central America (Ramírez and Pringle 1998). However, existing data are problematic for evaluating RCC predictions because, similar to most FFG studies in the temperate zone, these tropical studies have (*i*) been based on macroinvertebrate abundances, (*ii*) excluded decapods, (*iii*) been conducted in systems highly modified by humans, and (or) (*iv*) limited sampling to a single type of habitat (e.g., riffles).

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Conclusions from functional group analyses can vary substantially with the metric used (Fisher 1995). Biomass and production are appropriate metrics to use for evaluating the RCC and indicating ecosystem attributes (Barmuta and Lake 1982; Cummins and Merritt 2001). Abundance and taxonomic diversity can be misleading (Grubaugh et al. 1996). Excluding shrimps and crabs from analyses, or not sampling them with appropriate methods, is especially problematic in the tropics because these decapods often represent important primary consumers and detritivores. Analyses of highly impacted tropical systems confound biome and human impact and are problematic because the RCC attempted to describe unperturbed longitudinal patterns.

Functional group RCC analyses also must examine average or characteristic fauna at each site; this requires sampling of all major habitats (Minshall et al. 1985; Grubaugh et al. 1996). Our data support this contention. Río Mameyes trends in relative contributions of habitat-weighted FFGs match habitat-specific trends for pools but not for boulder–bedrock riffles. Macroinvertebrate sampling is often limited to riffles, but if we had limited our sampling to boulder–bedrock riffles, we would have erroneously concluded that the Río Mameyes continuum does not match any RCC predictions for FFGs.

Why does the Río Mameyes continuum not follow the RCC prediction for filterers?

Our finding that filterers do not conform to RCC predictions may be due to several challenges in our application of the FFG approach. First, we generally identified non-decapod invertebrates to the family or subfamily level. Several researchers have argued that genus- or species-level identifications are necessary to assess FFGs (Plague et al. 1998; Lenat and Resh 2001). However, greater resolution of identifications would be unlikely to alter our results because biomass of decapods and snails outweighed other invertebrate biomass by two orders of magnitude.

A second and more important challenge is the high abundance of shrimps, which are capable of more than one mode of feeding. Applying FFGs to these generalists is problematic because solid data on which to base apportionment of FFG membership are lacking (c.f., Hawkins and MacMahon 1989). We apportioned shrimp biomass equivalently among each feeding mode known for adults; however, our analysis could be improved with detailed studies on shrimp FFG apportionments. Our feeding mode apportionment also assumes that the proportion of time spent by shrimps in each feeding mode does not vary between juveniles and adults or longitudinally. However, feeding mode is known to vary with age for many macroinvertebrates (Cummins 1973; Davies et al. 1995; Ladle and Westlake 1995), and shrimp diets may change with elevation because of longitudinal variation in predators or food resources (Cushing and Allan 2001; March et al. 2001).

We found broad agreement with many RCC predictions, despite high abundances of generalist shrimps. These findings contrast with current thinking about generalist feeders. Facultative relationships with food categories are thought to make generalist macroinvertebrates less reliable indicators of ecosystem conditions (e.g., autotrophy vs. heterotrophy, CPOM vs. FPOM; Mihuc and Minshall 1995; Cummins and Merritt 2001), indicative of shifting availability of different types of food resources (Dodds et al. 2004), and problematic in efforts to evaluate the RCC (Cooper 1996; Plague et al. 1998; Cushing and Allan 2001). In fact, dominance by generalists is a major feature of regions such as New Zealand (Winterbourn 1995) and Australia (Lake 1995), which are the focus of classic debates about the applicability of the RCC to non-northern-temperate streams.

A third consideration in our application of FFGs is that we excluded fishes from our analysis. Excluding fishes in FFG- and RCC-related studies may be particularly problematic in the tropics where fishes are often important herbivores and detritivores (Lowe-McConnell 1987; Wootton and Oemke 1992; Lévêque 1995). The algivorous goby, *Sicydium plumieri*, is abundant in the middle of the Río Mameyes continuum and including it in the scraper category could alter our findings. However, a preliminary analysis, based on (*i*) visual estimates of *Sicydium* lengths from snorkeling, (*ii*) measured *Sicydium* lengths from electroshocking, and (*iii*) a *Sicydium* length – wet mass regression (Nieves 1998), indicates that including algivorous gobies as scrapers would not alter our overall longitudinal patterns in proportional representation of FFGs.

A fourth challenge in our analysis is the relative degree of human disturbance of the Río Mameyes drainage. It is one of the least human-modified drainages in the Caribbean and thus one of the closest indicators of unperturbed longitudinal patterns possible for running waters in the Caribbean. However, the drainage is affected by human activities (e.g., past agricultural land use at low and mid-elevations and present urban–suburban land use in the lowlands (Thomlinson et al. 1996; Clark and Wilcock 2000; Grau et al. 2003), the exotic snail, *T. granifera*, introduced in the 1950s (Pyron and Covich 2003), and freshwater shrimp harvest (Greathouse et al. 2005)). Thus, it may be problematic to use the Río Mameyes continuum to evaluate the RCC, which is generally regarded as a theory applying to pristine rivers, but this challenge is inherent in many RCC studies, including the use of human-modified systems of North America in the development of the RCC (Statzner and Higler 1985) and the use of human-modified systems of New Zealand in criticisms of the RCC (Davies et al. 1995).

Despite the aforementioned challenges, we believe our results are reliable and the decrease in filterers downstream is not due to a problem in our methods or analysis. This leads to the question of whether the pattern of filterers represents a contradiction of the RCC. We suggest that it is not a contradiction but instead a potential refinement of the RCC (sensu Minshall et al. 1992). The pattern appears to fit the framework outlined by Minshall et al. (1985) for a biome-related variation on the central RCC theme of longitudinal FFG patterns following longitudinal patterns in basal resources, which in turn reflect the physical gradient. Based on our data, we cannot draw conclusions about overall organic matter dynamics in light of RCC predictions on ratios of fine vs. coarse allochthonous resources because we did not measure organic matter in transport. However, we found that the ratio of fine to coarse BOM decreases downstream, which is opposite of the RCC prediction for the ratio of fine to coarse

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particulate organic matter (POM) in temperate forested streams. This suggests that low availability of coarse detritus relative to availability of fine POM in headwaters may explain the high representation of filterers in the Río Mameyes headwaters.

Patterns in detrital resources (and thus FFGs) of Río Mameyes may differ from those in temperate systems because tropical climates likely cause different patterns in organic matter inputs, retention, and decay (de la Rosa 1995). Terrestrial inputs of FPOM vs. CPOM to other tropical streams are thought to be skewed towards fines. CPOM inputs may be reduced because tropical temperatures and humidity and retention of CPOM in rainforest canopy structures (e.g., hyphae networks, bromeliads) cause high terrestrial decay rates of leaves (Minshall et al. 1985; Covich 1988*b*; Yule 1996*b*). In fact, our results are similar to those of Yule (1996*a*, 1996*b*) who studied proportional abundances of FFGs in a headwater vs. a lowland site in Papua New Guinea. Filterers decreased downstream in New Guinea, and their dominance in the headwaters was attributed to terrestrial decomposition causing stream inputs to be dominated by FPOM rather than CPOM. Puerto Rico's tropical climate may also affect the relative availability of fine vs. coarse POM by affecting in-stream processes (e.g., poor retention and high in-stream abrasion of CPOM and debris dams due to flash floods and warm temperatures; Buzby 1998; Merriam et al. 2002). Alternatively, the food quality of leaf inputs may be similar to those of other tropical streams, where high concentrations of secondary compounds are thought to limit shredder biomass (Stout 1989).

The truncated continuum patterns that we observed for scrapers and shredders match findings on longitudinal patterns in autotrophic vs. allochthonous resources in relation to canopy cover (Ortiz-Zayas et al. 2005). This is additional evidence that Río Mameyes FFG patterns follow patterns in basal resources. The drainage is heterotrophic along its entire length (ratios of primary production to community respiration (P/R) < 1; Ortiz-Zayas et al. 2005). However, there is a large increase in primary production and only a small increase in community respiration downstream. Thus, P/R increases along the gradient consistent with the downstream decrease in canopy cover and the RCC prediction for P/R from headwaters to mid-orders.

For possible explanations of the filterer pattern, effects of predators are an alternative to filterers tracking basal resources. This alternative would represent a major and perhaps long overdue refinement of the RCC, which is essentially a "bottom-up" theory (i.e., food resources control consumer distributions) (Dettmers et al. 2001). Attributing the filterer pattern to patterns in fine vs. coarse basal resources would imply that high atyid shrimp abundances at high elevations are a consequence of these patterns. However, there is a long-standing hypothesis that waterfalls blocking upstream migration of predatory fishes cause observed atyid distributions. If high atyid abundance upstream from waterfalls is due to a release from fish predation, then the Río Mameyes drainage may be a system in which longitudinal patterns in FFGs are also controlled by top-down factors. Other systems in which a downstream increase in fish predation is thought to affect longitudinal FFG patterns are the headwaters of the Medway River (an acid stream system in southeast England; Townsend and Hildrew 1984) and the Little Tennessee River – Coweeta Creek continuum (Grubaugh et al. 1996).

Do shrimps cause longitudinal variation in benthic resources?

In situ manipulative experiments (e.g., Pringle et al. 1999; Crowl et al. 2001; March et al. 2001) have demonstrated dramatic effects of atyid and *Xiphocaris* shrimps on leaf decay rates and standing stocks of epilithic chlorophyll *a*, FBOM, FBIM (i.e., fine sediments), and aquatic insects. Thus, we examined whether chlorophyll *a*, FBOM, FBIM, CBOM, and aquatic insects are at low levels where atyid and *Xiphocaris* biomass is high (above the waterfall) and are increased below the waterfall where these shrimps are at low abundances and biomass. We found no negative correlations between any benthic resources and biomass of atyids and *Xiphocaris*, and we did not observe clear increases in any benthic resources below the waterfall barrier to predatory fish. In fact, epilithic chlorophyll *a* showed a significant downstream decrease. Moreover, there were positive correlations between biomass of invertebrates, BOM, and chlorophyll *a* similar to those observed by Grubaugh et al. (1996). These correlations indicate that invertebrates are tracking food resources.

Along a longitudinal gradient encompassing a waterfall in a neighboring drainage, March et al. (2002) found that effects of shrimp exclusion on algae, organic matter, and insects varied. There were no effects in a low-elevation site with abundant grazing snails (primarily native), whereas effects at mid- and high-elevation sites were significant. A downstream decrease in chlorophyll *a* was also observed. The negative correlation we observed between chlorophyll *a* and snail biomass (~95% native snails) suggests that grazing by abundant snails at low elevations is causing the chlorophyll *a* pattern. Likewise, the negative correlation between atyid shrimps and snails is consistent with the hypothesis of March et al. (2002) that high abundances of shrimps at high elevations may be due to a release from competition with snails. This hypothesis and hypotheses about snail grazing maintaining low standing stocks of algae, organic matter, and insects deserves detailed experimental study in the tropics.

We further hypothesize that grazing by the high abundance of algivorous gobies in the middle reaches of Río Mameyes is an important factor in maintaining low standing stocks of epilithic chlorophyll *a*, FBOM, and FBIM. In other Puerto Rican streams where *Sicydium* are not prevalent, epilithic FBOM and FBIM show a dramatic pattern in relation to predatory fish barriers: thick layers of fines occur on rocks in pools with predatory fishes immediately below the waterfall, and rocks in pools above the waterfall are clean (E. Greathouse, personal observation). In contrast, rocks appeared clean at all of our sites both above and below the predatory fish barrier.

Significance

Our findings on FFGs, FBOM, and CBOM combined with those of Ortiz-Zayas et al. (2005) on P/R indicate that the Río Mameyes drainage conforms to the central theme of the

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RCC: changes in stream size determine changes in basal resources and consumers. However, our results also indicate that longitudinal patterns in FFGs in the Río Mameyes are influenced by top-down control, a mechanism that is not currently considered in RCC literature. Findings for the Río Mameyes likely have wide application because the basic geomorphology and longitudinal distributions of diadromous fauna (fishes, decapods, and snails) in the Río Mameyes are characteristic of tropical insular and coastal streams throughout the world (Smith et al. 2003). As in the Río Mameyes, tropical insular and coastal streams across the Caribbean, Latin America, the Pacific islands, and Asia have high abundances of snails and algivorous gobies at low and mid-elevations and high shrimp abundances above waterfalls that block upstream migration of predatory fishes (e.g., Hunte 1978; Lyons and Schneider 1990; Craig 2003).

Comparing the Río Mameyes and Coweeta Creek continuums provides a more detailed understanding of how a model tropical island stream differs from a model temperate continuum. However, the extent to which these findings can be generalized, and applied to refining the RCC, is unclear because our study represents a comparison of only two case studies, and we focused on using catchment area as a measure of stream size in our comparisons. For example, it is unknown whether the FFG equations in the Coweeta Creek – Little Tennessee River continuum are representative of other temperate systems. It is also unclear the extent to which results would have differed had we made comparisons using other possible measures of position along the continuums, such as stream order, runoff, distance, slope, etc.

Differences among the Río Mameyes, the Little Tennessee River, and the RCC may be due to the Río Mameyes being an island stream or a tropical stream or they may be due to another reason. Comparing a single tropical island stream with a single temperate stream limits our ability to determine which factors cause observed differences. This limitation is not only attributable to our study design, but also reflects a paradox in RCC research. On the one hand, the RCC is an important concept in research on the ecology of streams: the original paper introducing the concept (Vannote et al. 1980) is the most-cited paper in benthic science (Resh and Kobzina 2003). On the other hand, the extent to which the RCC has made a difference in our understanding of aquatic ecology has been greatly debated since its original publication (e.g., Winterbourn et al. 1981; Minshall et al. 1985). Many have questioned whether the concept provides predictive power for making comparisons among sites or understanding system responses to disturbance at different points in stream networks. Proponents argue that the most powerful idea from the RCC is simply its provision of an organizing framework and a standard set of methods and measurements for conducting comparative longitudinal studies across biomes and stream types (e.g., Barmuta and Lake 1982; Minshall et al. 1985; Ortiz-Zayas et al. 2005). However, this potential power is unrealized because there are actually few longitudinal studies testing RCC predictions (especially on FFG biomass) in any biome, let alone comparative longitudinal studies using similar methods across a broad array of biomes. Comparisons across multiple examples of tropical, temperate, island, and continental streams, using multiple types of measures of position along the continuum (e.g., order, runoff, distance, etc.), would be necessary to determine the causes of the differences between the Río Mameyes and the Little Tennessee River, as well as the true potential of the RCC as an organizing concept in stream ecology. Such comparisons would also benefit conservation and management because they would allow us to incorporate insular tropical systems into our general understanding of lotic structure and function (Smith et al. 2003). Improved conservation and management of these systems is critical because the biological integrity of many tropical island streams, including Río Mameyes and its headwaters, is threatened by growing water demands (March et al. 2003), land use change (Brasher 2003), and our minimal understanding of insular tropical stream ecology (Smith et al. 2003).

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Appendix A

Table A1. Carapace and shell length–mass regressions determined for decapods and snails preserved in ~10% formaldehyde.

Taxon	*L*	*a*	*b*	% ash	R^2	*N*
Xiphocaris elongata	Carapace length	0.0001	3.042	9.1	0.97	64
Atya lanipes	Carapace length	0.0004	2.579	15.1	0.95	55
Non-gravid *Atya scabra*	Carapace length	0.0004	2.479	26.2	0.68	24
Gravid *Atya scabra*	Carapace length	0.0005	2.500	23.1	0.82	23
Non-gravid *Atya innocous*	Carapace length	0.0001	2.904	27.5	0.95	21
Gravid *Atya innocous*	Carapace length	0.0001	3.179	24.2	0.93	17
Juvenile *Atya* spp.	Carapace length	0.0012	1.450	19.0	0.47	12
Micratya poeyi	Carapace length	0.0006	1.881	13.8	0.74	57
Non-gravid *Macrobrachium*	Carapace length	0.0004	2.636	12.7	0.96	39
Gravid *Macrobrachium* spp.	Carapace length	0.0002	3.016	13.3	0.98	18
Epilobocera sinuatifrons	Carapace length	0.00005	3.324	47.6	0.98	35
Thiara granifera	Shell length	0.00002	2.618	87.6	0.95	78
Neritina spp.	Shell length	0.000008	3.532	83.2	0.94	73

Note: AFDM = aL^b, where *L* is either carapace length or shell length in mm and AFDM is ash-free dry mass in grams; % ash, percent ash content (includes shells for snails); *N*, number of individuals used in determining regression. Carapace length was the postorbital carapace length (Hobbs 1991).

Appendix B. Predatory fishes, standing stocks of macroinvertebrates and basal resources, and proportional representation of habitats in sampled sites (1–9) along the Río Mameyes continuum.

Tables B1–B6 appear on pages 150–152.

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Table B1. Predatory fishes.

	Riffle									Pool								Run
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Anguilla rostrata					×		×	×	×					×		×	×	
Agonostomous monticola					×		×	×	×					×	×	×		×
Electridae					×		×	×	×					×	×	×	×	×

Note: ×, present in electroshocking samples or observations.
[a]Site number.

Table B2. Decapods (g AFDM·m^{-2}).

	Riffle									Pool								Run
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Atyidae	1.0	7.6	8.8	10.1	<0.1	<0.1	<0.1	<0.1	0.1	2.9	1.1	2.4	0.1				<0.1	<0.1
Xiphocaris elongata		0.8	0.2	0.4	<0.1		<0.1	<0.1	<0.1	0.3	3.0	1.9	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Macrobrachium spp.			<0.1	0.2	<0.1	0.3	0.3	0.3	0.3		<0.1	0.3	0.5	2.9	<0.1	<0.1	<0.1	0.2
Epilobocera sinuatifrons	0.3	<0.1		<0.1	<0.1		<0.1	<0.1			0.4	2.7	<0.1			0.6		

Note: Atyidae, *Atya lanipes*, *A. innocous*, *A. scabra*, *Micratya poeyi*, and juvenile *Atya* spp. AFDM, ash-free dry mass.
[a]Site number.

Table B3. Non-decapod invertebrates (mg AFDM·m^{-2}).

	Riffle									Pool								Cobble	*Hydrilla*
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	9
Phanocerus spp. Elmidae (C)	<1	3		<1	1		<1	6	<1		<1	1	<1	<1	<1	<1	1		
Other Elmidae (C)			5	<1	1	<1	<1	159	159	2		<1	<1	1	3	4	11		69
Blephariceridae (D)					65									<1					
Chironomidae (D)	6	2	216	1	8	7	2	17	13	15	<1	1	4	14	6	4	2	<1	80
Simuliidae (D)	31	<1		1	3	<1	1	<1	<1			<1							
Baetidae (E)	<1	5	<1	<1	<1	<1		<1	16		6	13	7	<1	1	<1	<1	2	741
Leptophlebiidae (E)	<1	15	<1					61	12		<1	3	1	<1	1	6	6	7	1
Crambidae (L)			124	<1	4	26	2	1			<1			<1	<1	<1	<1		
Libellulidae (O)	1	4						<1		79		<1	4	<1		<1	<1		<1
Hydropsychidae (T)	<1		49			<1					<1								
Hydroptilidae (T)	52	<1	66	6	585	29	<1	20	36			<1	<1	2	<1	<1	<1		94
Philopotamidae (T)	<1		13		6	1	<1	235	299				<1		<1	<1			<1
Neritina spp. (snail)								2388	4500					5694	1758	1476	3890	9631	24 922
Thiara granifera (snail)								2	42					112	228	183		63	1 736
Others	17	9	1	3	7	16	<1	10	6	4	<1	12	<1	1	6	3	3	<1	4

Note: AFDM, ash-free dry mass; cobble, cobble habitat in runs; *Hydrilla*, *Hydrilla* macrophytes in runs; C, Coleoptera; D, Diptera; E, Ephemeroptera; H, Hemiptera; L, Lepidoptera; O, Odonata; T, Trichoptera.
[a]Site number.

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Table B4. Functional feeding group biomass.

	Riffle									Pool								Run
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Scrapers, D	0.3	2.8	2.5	3.3	<0.1	<0.1	<0.1	<0.1	<0.1	1.1	1.4	1.4	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Scrapers, N	37	16	161	6	365	41	3	2512	4655	<1	3	10	5	5809	1991	1665	3900	17.7
Shredders, D		0.3	<0.1	0.1	<0.1		<0.1	<0.1	<0.1	0.1	1.0	0.6	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Shredders, N	<1	3		<1	1		<1	6	<1		<1	1	<1	<1	<1	<1	2	
Collector–gatherers, D	0.5	2.8	2.5	3.4	<0.1	0.2	0.2	0.3	0.2	1.1	1.6	2.9	0.3	1.4	<0.1	0.3	<0.1	0.2
Collector–gatherers, N	39	14	252	5	304	22.3	3	145	128	18	4	20	8	16	9	10	11	0.3
Collector–filterers, D	0.3	2.5	3.9	3.8	<0.1	<0.1	<0.1	<0.1	<0.1	1.0	0.4	0.8	<0.1				<0.1	<0.1
Collector–filterers, N	32	<1	62	1	9	2	1	244	299	<1	<1	9	<1	<1	<1	<1	<1	<1
Predators, D	0.2	<0.1	<0.1	<0.1	<0.1	0.2	0.2	0.3	0.2		0.2	1.5	0.2	1.4	<0.1	0.3	<0.1	0.1
Predators, N	3	6	<1	<1	1	15.4	<1	2	1	81	<1	1	5	<1	4	3	4	<1

Note: AFDM, ash-free dry mass; D, decapods (g AFDM·m^{-2}); N, non-decapod invertebrates (mg AFDM·m^{-2}).
[a]Site number.

Table B5. Basal resources.

	Riffle									Pool								Cobble	*Hydrilla*
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	9
Chlorophyll *a* (mg·m^{-2})	4.3	7.9	5.4	15.3	1.5	0.9	0.9	0.7	0.2	4.4	2.2	1.5	6.2	2.0	1.8	0.6	0.7	0.2	—
VFBOM (g AFDM·m^{-2})	1.0	2.8	2.2	2.1	0.7	0.8	1.3	1.2	0.8	73.2	7.1	20.6	5.8	11.3	13.4	9.7	26.2	0.7	68.7
MFBOM (g AFDM·m^{-2})	5.4	46.2	2.6	0.2	0.6	0.2	<0.1	1.2	5.6	249	1.3	1.1	0.5	0.2	0.9	0.5	0.4	0.2	5.4
CBOM (g AFDM·m^{-2})	88.6	9.3	0.4	<0.1	1.5	0.3	0.1	18.8	12.4	26.9	3.2	5.7	9.6	0.4	9.5	6.9	5.2	3.2	558
VFBIM (g·m^{-2})	1.9	11.5	2.2	0.6	0.4	0.6	0.1	0.3	0.8	255	11.9	18.9	9.4	3.3	20.2	11.1	19.2	0.8	381
MFBIM (g·m^{-2})	203	599	0.7	<0.1	0.5	0.2	0.1	10.7	25.2	6736	0.4	1.0	0.8	0.1	0.2	0.2	0.1	0.4	9.6

Note: VF, very fine (<250 µm); MF, medium fine (<1 mm, >250 µm); C, coarse (>1 mm); B, benthic; OM, organic matter; IM, inorganic matter; AFDM, ash-free dry mass.
[a]Site number.

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Table B6. Proportional representation of habitats.

	Riffle									Pool								Run	
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	
For decapod sampling	0.59	0.70	0.77	0.78	0.61	0.61	0.40	0.27	0.24	0.41	0.30	0.23	0.22	0.39	0.39	0.60	0.73	0.76	
For non-decapod invertebrate sampling																		Cobble	*Hydrilla*
Boulder–bedrock	0.32		0.60	0.76	0.52	0.53	0.29				0.17	0.15	0.14	0.23	0.30	0.43	0.46		
Sand										0.27									
Cobble		0.53						0.21	0.19									0.13	
Hydrilla macrophytes																			0.61

Note: Cobble, cobble habitat in runs; *Hydrilla*, *Hydrilla* macrophytes in runs.
[a]Site number.

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Effectiveness of marine reserves for large-scale fisheries management

Martin D. Smith, Junjie Zhang, and Felicia C. Coleman

Abstract: As more no-take marine reserves are established, the importance of evaluating effectiveness retrospectively is growing. This paper adapts methods from program evaluation to quantify the effects of establishing a marine reserve on fisheries using fishery-dependent data. The approach analyzes the effects of a policy at the individual vessel level and accommodates the coarse spatial resolution of fishing logbooks. It illuminates implicit assumptions in previous retrospective analyses of marine reserves that are unlikely to hold for large-scale fisheries. We illustrate the empirical model with an application to the Gulf of Mexico reef-fish fishery. Isolating the effects of reserves requires a full accounting of multiple gear production technologies, heterogeneity in vessel captain skill, spatial heterogeneity of fish stocks, seasonal patterns in abundance, the effects of coexisting management policies, and the possibility that the harvest sector anticipates reserve establishment. We find that the effect of two recently established marine reserves on catch is negative and trending downward, though the reserves have only been in place for 4.5 years.

Résumé : À mesure que les réserves marines sans récolte deviennent de plus en plus nombreuses, il est d'autant plus important de pouvoir évaluer leur efficacité de façon rétrospective. Notre travail adapte des méthodes d'évaluation de programmes afin de quantifier, à l'aide de données reliées à la pêche, les effets de l'établissement d'une réserve marine sur les pêches commerciales. Notre méthodologie analyse les effets des politiques au niveau du navire individuel et s'accommode de la résolution spatiale grossière obtenue à partir des livres de bord de pêche. Elle précise certaines des présuppositions implicites dans les analyses rétrospectives antérieures de réserves marines, qui ne valent vraisemblablement pas pour les pêches à grande échelle. Nous illustrons notre modèle empirique en l'appliquant à la pêche commerciale sur les récifs du golfe du Mexique. Pour isoler les effets des réserves, il faut tenir un compte complet des technologies multiples de production des engins de pêche, de l'hétérogénéité des compétences des capitaines de bateau, de l'hétérogénéité spatiale des stocks de poissons, des patrons saisonniers d'abondance, des effets de politiques de gestion parallèles et de la possibilité que le milieu de la pêche ait prévu l'établissement de la réserve. Nous trouvons que les effets de deux réserves marines récemment établies sur les récoltes sont négatives et ont tendance à diminuer, bien que ces réserves ne soient en place que depuis 4,5 années.

[Traduit par la Rédaction]

Introduction

The dominant paradigm in fisheries policy is undergoing a transformation from one that views regional fish stocks as single entities towards one that increasingly acknowledges both the importance of these stocks as integral components of ecosystems and the importance of spatial heterogeneity and spatial processes in management (Ecological Society of America (ESA) 1998; National Marine Fisheries Service (NMFS) 1999). This transformation has led to intense interest in establishing marine reserves around the world (ESA 2003). Marine reserves or no-take areas, a particular type of marine protected area in which exploitation is prohibited, have long been an important part of marine conservation. Considerable attention in recent years has focused on using reserves explicitly to manage commercial fishery yields (Bohnsack 1998; Carr and Reed 1993; National Research Council 2001). As more reserves are established and empirical data become available, it is critical to evaluate their performance and continuously assess the overall potential of reserves to address sustainability and production problems in fisheries management.

The theoretical basis for establishing marine reserves for fisheries management is straightforward. A marine reserve, by eliminating fishing pressure in a particular area, allows biomass in the closed area to rebuild, through both growth and reproduction, and eventually spill out of the reserve into the surrounding open areas (Polacheck 1990). For many spe-

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cies of fish, larger individuals generate more offspring than their smaller counterparts, leading to greater reproductive success (Bohnsack 1998; Koops et al. 2004). There is also a growing body of evidence that older fish have more viable offspring than younger fish (Berkeley et al. 2004*a*, 2004*b*). Thus, a reserve could produce significant biological returns (Smith 2004) such that long-term gains from the reserve outweigh losses resulting from the reduction in fishing area (Roberts and Polunin 2001), as long as the reserve captures source rather than sink areas (Crowder et al. 2000). The reserve design literature asks questions about the ecological, oceanographic, and economic circumstances under which reserves may benefit fisheries through increased or stabilized yields (Gerber et al. 2003; Smith and Wilen 2003; Sanchirico 2004). While these papers suggest ex ante when we might expect a reserve to generate catch increases, they provide little guidance on how to measure the short-run and long-run changes in catch ex post.

In contrast, we ask how fisheries scientists would know if reserves are effective once they are established. Previous researchers have acknowledged that retrospective analyses are important but that few such analyses exist for marine reserves (Hilborn et al. 2004; Sale et al. 2005). What our study highlights is that responses of the harvest sector cast doubt on the ability of researchers to implement a before–after control–impact pair (BACIP) marine reserve experimental design.

We view a marine reserve as a policy treatment that may or may not affect fishing in the broader zone in which it is placed. The goal then is to measure the treatment effect. However, fishing pressure outside the reserve is not experimentally controlled, and this lack of control complicates the problem of measuring the treatment effect. For management of fisheries yields, the treatment site is an area near a reserve where economic benefits following from enhanced productivity could materialize for fisheries, whereas the reference (or control) site is an area far from the reserve where the fishery is presumably unaffected by the establishment of a reserve. When increasing catch is a goal of management, the definition of a reference site is obscured by the fact that fishing pressure at that site will not necessarily be the same before and after reserve formation. As a consequence, non-experimental methods are necessary for retrospective analyses, and a marine reserve for fisheries management is more appropriately analyzed as a social program rather than as a randomized experimental trial.

When a marine reserve is established and there are changes in measured fishery outcomes, determining the effectiveness of the reserve amounts to determining which of these changes are attributable to the policy and which are attributable to other factors. For judging a reserve, Gell and Roberts (2003, p. 453) suggest a " 'gold standard' of higher overall catches with reserves than without, in spite of a reduced fishing area". Though we agree with the sentiment of this gold standard, we seek to make it more explicit so that reserve evaluations are robust to a behavioral response of the fishing fleet. Ideally, determining the effectiveness of a reserve for fisheries management would test whether the reserve causes harvestable biomass to increase. This means that harvestable biomass outside the reserve needs to increase enough to offset what is closed off within the reserve. Because stocks are unobservable (latent) in fishery-dependent data, we use catch as an indicator of harvestable biomass.

Higher overall catches could indicate an effective reserve for fisheries management, but higher overall catches are neither necessary nor sufficient for effectiveness. Observed higher overall catch rates do not necessarily mean that the reserve is effective, and observed lower catch rates do not necessarily mean that it is a failure; conditional catches are what matter, and the researcher must control for possible selection effects at treated and reference sites. For instance, higher total catches could reflect a change in fleet composition to higher skilled fishermen or larger boats near the reserve. This case would not indicate an effective reserve in our model. Lower total catches could mean the opposite and suggest that the reserve is not necessarily a failure in our model.

To be more specific, evaluating effectiveness requires answering the following hypothetical question: did a particular vessel deploying a particular type and quantity of gear catch more in an area near the reserve after formation of the reserve than it would have caught had the reserve never been established? We submit that a positive answer to this question should be the gold standard for evaluating whether a reserve generates fishery benefits. Addressing this type of hypothetical question is central in program evaluation of environmental policy (Bennear and Coglianese 2005), but this literature has not yet been applied to fisheries policy.

The intuition for our proposed gold standard is that if nothing changes in the fishery except the policy change of forming a reserve, then fishermen would be catching more with the policy than without it. Of course, we cannot hold everything constant in a physical sense in the way that we would hold features of the system constant in a randomized experiment, nor can we directly observe the counterfactual case of what would have happened had the reserve not been established. In practice, we build up the counterfactual statistically by analyzing whether a particular vessel conditional on a range of factors would catch more near the reserve (in the treatment area) vs. far from the reserve (in the reference area). Our model does have aggregative properties in the sense that total catches from a reserve with a positive treatment effect would increase if everything else stays constant. That is, if there are no behavioral adjustments or selection effects, our model reaches the same conclusion about the effectiveness of a reserve as previous models that focus on overall catches.

To add to intuition, consider a hypothetical case from labor economics in which a voluntary job-training program is initiated at the onset of a recession. We would like to test whether the program decreases unemployment. Suppose further that the actual unemployment rate increases after the program for individuals enrolled in the training program (the treatment group) and for individuals not enrolled (the control group), but the increase is greater for the control group. If we simply measure total unemployment before and after the program, we would conclude that the program is a failure. If we compare the increase in unemployment between treated and control groups, we conclude that the policy is a success. However, this conclusion could be spurious if people who enrolled in the training program were different from those

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who did not enroll; enrollees might have more education (an observable characteristic) or simply be more motivated (an unobservable characteristic). This is the selection problem that plagues BACIP for marine reserve design.

To isolate the policy effects of marine reserves for large-scale fisheries management, our approach is to consider whether individual fishery participants receive "treatment" depending on whether they fish near or far from the newly established reserve. This allows us to consider how measuring the treatment effect of a marine reserve depends on the composition of the treatment and comparison groups, i.e., the individuals fishing near and far from a reserve. We develop a descriptive panel data model with an application to two recently established marine reserves in the Gulf of Mexico reef-fish fishery. By estimating an individual-level model, incorporating heterogeneity, and conditioning on the complexity of the pre-existing fishery management system, our model is more general than other retrospective analyses of marine reserve formation. Specifically, we show that isolating the effects of marine reserves on fisheries requires knowledge of the spatial scope of reserve spillovers, as well as a full accounting of multiple gear production technologies, heterogeneity in vessel captain skill, spatial heterogeneity of the fish stocks, seasonal patterns in abundance, the effects of coexisting management policies, and the possibility that the harvest sector anticipates the establishment of a reserve. All of these factors confound the problem of identifying BACIP for marine reserve design. Even if researchers are not interested in the fishery-related effects of reserves per se and they only seek to measure the ecological effects, the impact of the harvest sector on reference sites cannot be ignored. Our empirical results do not provide a definitive answer as to whether the marine reserves that we analyze have benefited fisheries, but they illustrate a number of important empirical issues that have not been addressed in previous studies. Our model ultimately highlights the types of data that future researchers will need to collect to analyze the effects of establishing reserves retrospectively.

Below we describe our empirical setting: the Gulf of Mexico reef-fish fishery. We then develop a descriptive panel data model to test the fishery effects of a reserve. We show that our model nests the before–after retrospective analyses of catch per unit effort (CPUE) that are currently in the literature. We subsequently present results of our model using data from Gulf of Mexico fisheries logbooks. Finally, we discuss our results and suggest directions for future research.

Materials and methods

Empirical setting — the Gulf of Mexico reef-fish complex

The Gulf of Mexico reef-fish complex presents managers with enormous challenges. There are 62 reef-fish species commercially harvested, including 11 grouper species and 10 snapper species, with a wide range of gears. The most common gears are hook and line (including handlines, electric bandit reels, buoy gear, and conventional rod and reel), bottom long line, and traps (although traps are being phased out completely over the next couple of years). Existing management includes limited entry (there are currently approximately 1200 federal commercial Gulf of Mexico reef-fish permit holders), size limits, trip limits, season closures, quota management, and more recently, marine reserves. Only a fraction of permitted vessels regularly engage in commercial reef-fish fishing. For example, 25% of vessels account for 75% of fishing trips over the 1993–2002 period.

Economically important species such as gag (*Mycteroperca microlepis*), scamp (*M. phenax*), and red grouper (*Epinephenlus morio*) could gain some long-run biological benefits from marine reserves. These species are long-lived, slow-growing protogynous hermaphrodites (Coleman et al. 2000). Protogynous hermaphrodites mature first as females and then transform to males later in life. Because fishing tends to select for larger individuals, it tends to select for males. This selection reduces male-to-female sex ratios (Coleman et al. 1996; McGovern et al. 1998), and some traditional fisheries management tools, particularly size limits, may exacerbate this effect. For Gulf of Mexico gag, the percentage of males from the 1970s to the 1990s has declined from 17% to 2% (Coleman et al. 2000). The same decline does not appear in red groupers, which do not aggregate to spawn (Coleman et al. 1996).

The two marine reserves in the Gulf of Mexico that we study (Madison–Swanson Marine Reserve and Steamboat Lumps Marine Reserve) went into effect in June 2000 to address concerns about this skewed sex ratio. They were announced to the fishing community 1 year before being established. They were authorized as experimental reserves with a sunset of 4 years and were recently reauthorized for an additional 6 years, based exclusively on biological data within and outside of each reserve and anecdotal information about the fishery outside each reserve. To date, there have been no systematic evaluations of these reserves as management tools, and understanding their performance will be critical for future reauthorizations.

The reserves are located in two of the 13 distinct NMFS fisheries statistical zones in the Gulf of Mexico (Fig. 1). These two zones represent the heart of the gag fishery in the Gulf of Mexico. Madison Swanson is located in zone 8, comprising 115 square nautical miles (n.mi^2) of this 9570 n.mi^2 zone, whereas Steamboat Lumps is located in zone 6, comprising 104 n.mi^2 of this 8100 n.mi^2 zone. Each reserve captures 1.2% and 1.3%, respectively, of the total area in the NMFS statistical zone within which they occur. There is, thus, substantial fishable area left open within each of the statistical zones, as well as elsewhere on the West Florida Shelf. However, percentage area is misleading in a fisheries context, because not all ocean bottom is alike. The reserves in question are located in deep water along the continental shelf edge and contain distinct patch reef formations where reef fish aggregate in general and many grouper species aggregate to spawn (Koenig et al. 2000).

There is not a one-to-one relationship between NMFS fishing zones and what we might reasonably deem a patch from a bioeconomic perspective. The spatial resolution of the logbook data is extremely coarse, which is typical, and the NMFS fishing zones are spatial aggregates of the underlying biological and economic processes. Herein lies one of the more challenging empirical problems that we address in our model of individual vessel catch.

Complete fishing logbook data exist for all reef species in the Gulf of Mexico from 1993 through 2004. Thus, there are

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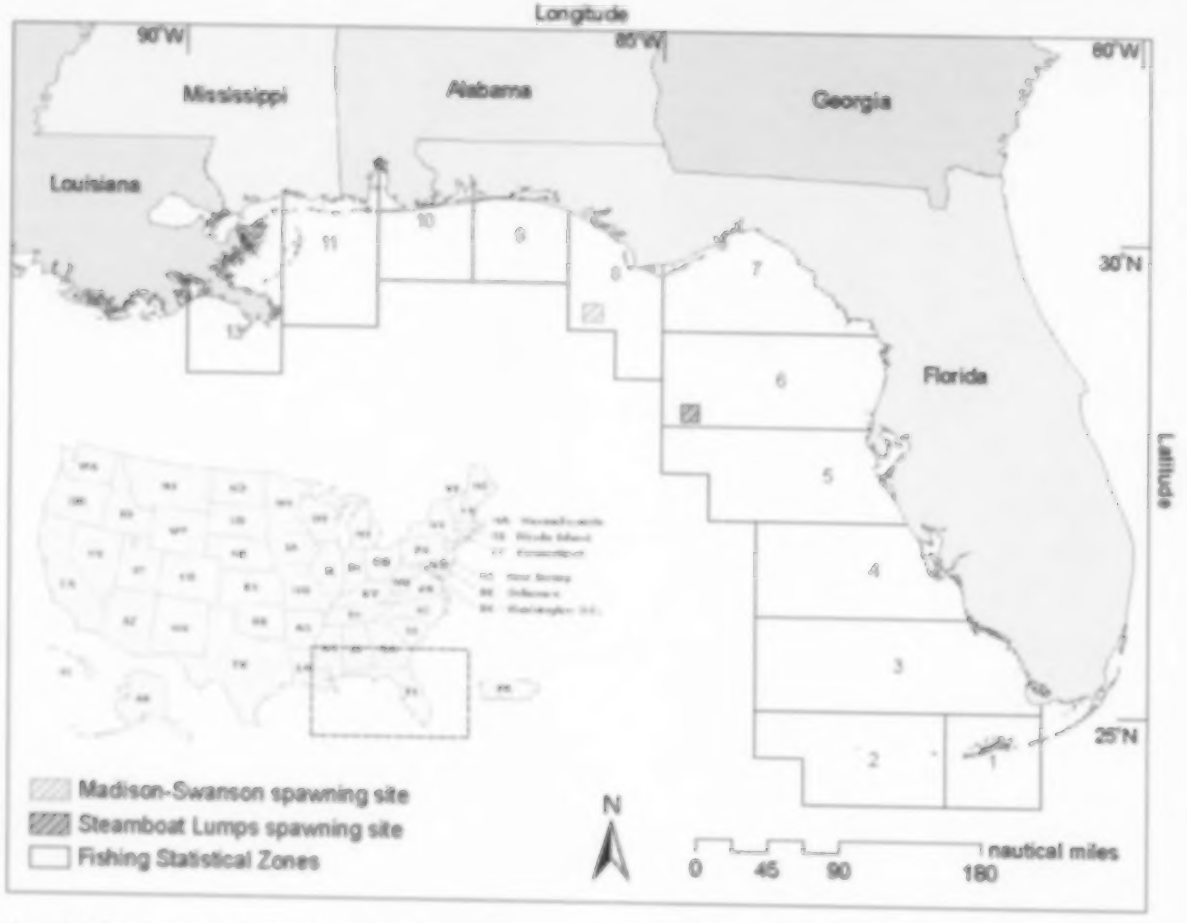
Fig. 1. Gulf of Mexico reef no-take marine reserves established in June 2000. Marine reserves are contained within National Marine Fisheries Service statistical zones.



substantial data before and after the policy change to assess reserve performance. We cut the data after October 2004 because some logbook records for 2004 may not have been submitted or processed in the most recent database that we received in February 2005. This leaves us with 142 months of data.

A panel data model of marine reserves for fisheries management

Before–after comparisons of catch rates most closely parallel the program evaluation literature in economics. A reserve is a policy treatment. The general area that contains the reserve is thus a treatment area (the area in which reserve effects are most likely to be realized), and the goal is to measure the treatment effect against some reference (an area remote enough to be unaffected by the reserve). We considered the two NMFS statistical zones that contain marine reserves (zones 6 and 8) as treatment zones and the remaining 11 as reference zones. Implicitly, our panel model assumes that spillovers and larval export effects materialize exclusively in those statistical zones containing the marine reserves.

To make the hidden assumptions of retrospective analyses more transparent and inclusive, we propose a more a general model that (*i*) accounts for exogenous effects on catch typically *absent* from other models and (*ii*) accounts for selection bias using selection on unobservables (Heckman and Hotz 1989). Let i index individual fishermen or fishing vessels, j index fishing zone, k index fishing gear type, m index month of the year, and t index time (in days). Denote aggregate reef fish catch as h, fishing effort as E — where effort is defined specific to the gear type (details are available from the authors) — and biomass as X, and define the catchability parameter as q and a fishery production function exponent as α. An individual's catch on a given day in a particular area is

$$(1) \qquad h_{i,j,k,t} = q_{i,j,k,m}(E_{i,j,k,t})^{\alpha_k} X_{j,t}$$

This form allows the curvature of the catch function to depend on gear type and allows for heterogeneity in catchability across individual vessels, fishing areas, and gear types. It also allows catchability to vary by month, which may be particularly important for species that aggregate seasonally to spawn.

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We do not observe the fish stock directly and, as in other retrospective analyses, must make an assumption about how it evolves over time in each location. In the absence of a policy treatment, we assume that there is an initial stock and a trend that are both spatially specific:

$$X_{j,t} = \bar{X}_j \exp[r_{j,t} t] \quad (2)$$

where r is the rate of change, which could be positive or negative depending on bioeconomic conditions. Now suppose that at $t = T$, a marine reserve is introduced. We define Z as an indicator variable that denotes when a reserve is in effect such that

$$Z_{j,t} = \begin{cases} 1 \text{ if there is a reserve in } j \text{ and } t \geq T \\ 0 \text{ if no reserve or } t < T \end{cases} \quad (3)$$

In a large-scale commercial fishery, we typically do not observe fishing activity with fine spatial resolution. For many federally managed fisheries in the United States, we observe fishing at the scale of a National Marine Fisheries Service statistical zone, which can be on the scale of 10 000 n.mi^2 (Fig. 1). Thus, we consider the placement of a marine reserve within the spatial context of these statistical zones.

If a reserve generates biomass through either spillovers or larval export, it might appear to stimulate growth in the zone that contains the reserve. However, because the reserve also closes off part of the fishing area, it might appear to affect the production function for fishermen. Whether this effect reduces catch in a measurable way is an empirical question that can be tested with our model by introducing ϕ_1, a parameter that scales catch. Under the null hypothesis of no instantaneous effect, $\phi_1 = 1$. Another important empirical question is whether the reserve stimulates catch in the surrounding zone. This effect could only happen dynamically if stocks rebuild within the reserve and spill into open fishing areas through adult emigration or larval export that repopulates open fishing areas. We approximate this effect with a parameter ϕ_2 that introduces a change in the trend in eq. 2. Under the null hypothesis that the reserve has no effect, $\phi_2 = 0$. Substituting the reserve effects with eqs. 3 and 2 into eq. 1, we have

$$h_{i,j,k,t} = \phi_1^{Z_{j,t}} q_{i,j,k,m} (E_{i,j,k,t})^{\alpha_k} \bar{X}_j \exp[(r_{j,t} + \phi_2 Z_{j,t})t] \quad (4)$$

In essence, this model allows the reserve to influence biomass in the larger zone within which the reserve is embedded, but scaling the harvest function only permits harvesting in the open portion of the zone. This setup is consistent with many logbook data sets for which no-take fishery reserves do not correspond to an entire fishing zone.

At this juncture, it is important to reconsider how the model in eq. 4 relates back to theory of reserve design based on metapopulations. In our model, each fishing zone represents an entire metapopulation comprised of many patches. Recall that the motivation here is that we do not observe fishing activity at the subzone level, i.e., at the patch level. Thus, we have no means by which to parameterize dispersal among patches and only can generate qualitative predictions about the metapopulation as a whole. A reserve closes down one or several patches, but the zone is large enough to contain all of the relevant patches. This is a limitation of our approach but one that can be dealt with in the future as more spatially explicit data are collected.

A challenge for empirical implementation of our model is that policies typically do not go into effect for some period after they are announced. We might expect that fishing vessels would react to the announcement of a reserve at $t = \tau$ that will not go into effect until $t = T$. We define an instantaneous announcement effect (ρ_1), a trend announcement effect (ρ_2), and the indicator variable A

$$A_{j,t} = \begin{cases} 1 \text{ if reserve announced in } j \text{ and } \tau \leq t < T \\ 0 \text{ otherwise} \end{cases} \quad (5)$$

Adding announcement effects into eq. 4, we have

$$h_{i,j,k,t} = \rho_1^{A_{j,t}} \exp[\rho_2 A_{j,t} t] \phi_1^{Z_{j,t}} q_{i,j,k,m} (E_{i,j,k,t})^{\alpha_k} \times \bar{X}_j \exp[(r_{j,t} + \phi_2 Z_{j,t})t] \quad (6)$$

Another challenge in evaluating reserves for large-scale fisheries management is that reserves typically do not exist independent of other policies. If none of these other policies changes in the sample period, then estimating a model like the one in eq. 6 would be sufficient. However, if other policies do change, then they must be accounted for. Isolating the effects of reserves is theoretically still possible, because although marine reserves affect those individuals operating closest to them, most other management approaches, such as size limits, trip limits, and seasonal restrictions, affect the entire fishery. This allows us to specify an instantaneous effect, denoted by μ_1, and a trend, denoted by μ_2. Because the timing of the other policy may or may not coincide with the reserve, we define a separate indicator variable I for a policy change at t_0:

$$I_t = \begin{cases} 1 \text{ if "other" policy is in effect} \\ 0 \text{ otherwise} \end{cases} \quad (7)$$

Adding other policies into eq. 6 gives rise to

$$h_{i,j,k,t} = \rho_1^{A_{j,t}} \exp[\rho_2 A_{j,t} t] \mu_1^{I_t} \phi_1^{Z_{j,t}} q_{i,j,k,m} (E_{i,j,k,t})^{\alpha_k} \times \bar{X}_j \exp[(r_{j,t} + \phi_2 Z_{j,t} + \mu_2 I_t)t] \quad (8)$$

Even in the absence of other policies, we might include a fishery-wide indicator variable as in eq. 7 because it is still possible that the model otherwise would attribute an exogenous region-wide oceanic or biological event to the reserve treatment. This effect would come through as dampening individual zone-specific trends in the nontreated zones but picking up the shock directly in the treated zones. Thus, including this term is a difference-in-differences approach. See Bennear and Coglianese (2005) for a nontechnical discussion of program evaluation methods for environmental policy. We are measuring the difference between reference and treatment groups for the difference in catch before and after the policy. To correctly identify the treatment effect, this approach requires that the posttreatment trends in the absence of the policy would have been parallel.

The model in eq. 8 is quite general but suffers from a curse of dimensionality because the catchability coefficient is individual-, zone-, gear-, and month-specific. To reduce some dimensionality, we make the following simplification:

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$$(9)\quad q_{i,j,k,m} = q_i q_m q_{k,m} q_{j,m} q_{j,k}$$

We exclude a separate zone-specific catchability effect because it would not be separately identified from the baseline zone-specific stock $\widetilde{X}_j$. Substituting eq. 9 into eq. 8 leads to

$$(10)\quad h_{i,j,k,t} = \rho_1^{A_{j,t}} \exp[\rho_2 A_{j,t}] \mu_1^{I_t} \phi_1^{Z_{j,t}} q_i q_m q_{k,m} q_{j,m} q_{j,k} \times (E_{i,j,k,t})^{\alpha_k} \widetilde{X}_j \exp[(r_{j,t} + \phi_2 Z_{j,t} + \mu_2 I_t)t]$$

For the model above, we observe h, E, A, I, Z, and t. Everything else is a parameter to be estimated.

To derive an estimating equation, we take the natural log of eq. 10 and append an additive random shock $u_{i,j,k,t}$:

$$(11)\quad \ln(h_{i,j,k,t}) = \ln(\rho_1)A_{j,t} + \ln(\mu_1)I_t + \ln(\phi_1)Z_{j,t} + \ln(q_i) + \ln(q_m) + \ln(q_{k,m}) + \ln(q_{j,m}) + \ln(q_{j,k}) + \alpha_k \ln(E_{i,j,k,t}) + \ln(\widetilde{X}_j) + r_j t + \rho_2 A_{j,t} t + \phi_2 Z_{j,t} t + \mu_2 I_t t + u_{i,j,k,t}$$

This form is linear in all of the parameters. We are interested in comparing observed outcomes with the counterfactual case of a fishing vessel fishing in the same place at the same time without the reserve treatment. Because we cannot observe the counterfactual, we rely on data from fishing in reference sites. This introduces potential selection bias because individual effort, gear type, and zone choice might be correlated with the individual-specific error. To control for selection, we use selection on unobservables through fixed effects (Heckman and Hotz 1989) such that $u_{i,j,k,t} = \eta_i + \varepsilon_{i,j,k,t}$. Thus, we cannot separately identify the selection effect from the individual-specific catchability coefficient ($\ln(q_i)$ in the estimating equation), but lack of identification in this case does not inhibit our ability to draw inferences from the rest of the parameter estimates. The model is similar to the dynamic panel data model in the program evaluation literature used to study enterprise zones (Papke 1994). Assuming that the shocks are independently and identically distributed and $\mathrm{cov}(\ln(E_{i,j,k}), \varepsilon_{i,j,k,t}) = 0$, our fixed effects model can be estimated by demeaning the data and then using ordinary least squares. Note that estimating random effects would not involve demeaning the data and thus would not remove selection bias in this case. The total number of parameters depends on the number of fishing zones and gear types and unique combinations of month, gear, and zone that are identifiable.

We are now ready to compare our model with CPUE before–after analyses from the literature. We first address the curvature of the production function. Unless fishing effort before reserve establishment is identical, analyzing CPUE is equivalent to restricting all of the αs to 1. If the true $\alpha < 1$, then a decrease in effort postreserve will produce an increase in CPUE, even if the reserve is not generating any harvest benefits. Consider, for example, that Russ et al. (2004) find a total effort decline of 46% from 1986 to 1998–2001 and a 50% increase in CPUE over the same period. If $\alpha = 0.5$, then this effort decline would translate into a 36% increase in CPUE even if fishable biomass did not change. Thus, when there is a behavioral change postreserve, a change in CPUE may be falsely attributed to the policy. Moreover, by restricting the αs, other studies implicitly assume that all fishing gears are the same. This may be a reasonable assumption in studies of small-scale artisanal fisheries, but inferences for large-scale commercial fisheries need to account for gear differences.

Beyond generality of the production function, the model in eq. 11 allows analysts to distinguish habitat and other background effects from reserve effects. Including zone-specific effects $\widetilde{X}_j$ and trends r_j captures the influence of habitat that is independent of the reserve effects. Gell and Roberts (2003) raise this issue in discussing BACIP and point out the difficulty in resolving this issue with data sets on reserves. What we are suggesting is that the richness of fishery logbook data allow for a parameterization that can separate these effects if there is sufficient spatial resolution. Also, zone-specific trends in our model control for the possibility that apparent gains following a spatial closure are actually artifacts of upward trends in catch that were developing before reserve establishment.

Our model allows for several types of heterogeneity that previous studies assume do not matter. Perhaps most important here is heterogeneity across individuals. If individual fishing skill varies or vessel catching power varies in a way that is not controlled for by observables (e.g., captain catch history, vessel length, or vessel horsepower), changes in CPUE over time could simply reflect a change in the composition of the fishing fleet. Another source of heterogeneity is seasonality in catchability. CPUE studies can address this by always making before–after comparisons at the same time of year, but modeling seasonality directly allows for use of all observations rather than excluding before (after) observations that cannot be matched with after (before) observations in the same month. By interacting gear and month, our model also allows for particular gear types having more catching power than others when there are spawning aggregations.

Finally, our model traces out the full dynamic path of reserve impacts, not just the change at some arbitrary point in the future. This allows for before–after comparisons at each time step for whether a reserve has generated net benefits. For example, if the initial loss from establishing a reserve is large and rebuilding takes a long time, simple before–after comparisons may conclude that the reserve has not benefited fisheries when it simply has not had enough time. Our model allows us to examine the postreserve trend and the initial change.

Results

We estimate models for all reef-fish species aggregated together. There are eight commonly used gears in the data set, though not all of these catchability effects can be estimated because not all gears are deployed in every zone in every month. Certain policies target particular species or groups of species and therefore particular fishermen, but some of the reef-fish fishery participants are licensed to fish for all reef fish. Our empirical setting hence has overlapping policy layers. For instance, coincident with forming the two marine reserves in June 2000, the Gulf of Mexico Fisheries Management Council (GMFMC) increased the size limit for gag and black grouper (*Mycteroperca bonaci*) to 61 cm. Our fishery-wide postreserve shift and trend account for this effect, but it is important to note that we cannot distinguish it

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for causal inference from other coincident fishery-wide changes. Also, the GMFMC instituted a 1-month commercial grouper fishery closure from 15 February to 15 March each year beginning in 2001. We include a grouper closure dummy in the regressions to account for this effect, as well as month before and month after dummies to account for the possibility that the onset of the seasonal closure stimulates effort immediately before and after its occurrence.

Because red snapper is perhaps the most valuable reef-fish species in Gulf of Mexico and not all reef-fish vessels have equal access to snapper, we controlled for the effects of red snapper regulations on targeting strategies. We include a dummy variable for class 1 snapper vessels, which are allowed a trip limit of 909 kg. We also include a dummy to indicate when the snapper season is open and an interactive term for class 1 with snapper openings. Historical data for 1993–2000 snapper openings are from Waters (2001), and more recent data are provided directly by James R. Waters (National Marine Fisheries Service, 101 Pivers Island, Beaufort, NC 28516, USA).

We include two additional covariates to account for variable aspects of fishing intensity that are not controlled for by fixed effects or by gear-specific effort: (*i*) number of crew and (*ii*) number of vessels fishing in the zone. We would expect an increase in the number of crew to increase catch conditional on other factors. We would expect the number of vessels to be negative if there are crowding effects and positive if it captures seasonal effects, i.e., vessels tracking seasonal changes in abundance across zones. In this sense, number of vessels may proxy for temporal resolution of spawning aggregations that is finer than monthly dummies and month–zone interactions.

We report two sets of results (Table 1). The first is the full model including parameters that are not statistically significant. The full model for reef fish has 345 covariates. These are in addition to the 3173 vessel-specific fixed effects that are removed from the estimation through demeaning. The second set uses backward selection to eliminate statistically insignificant results based on *F* tests. After backwards selection, 290 covariates remain. Because there are so many regressors, our tables only report summaries of the gear–month, gear–zone, and zone–month dummies. Full results are available from the authors.

There are 162 634 actual trips contained in the logbook data. Because our time index is daily, we allocate multiday trips evenly across the days over which the trips span. Effort and catch for multizone trips are allocated evenly across zones. These factors inflate the number of observations to 404 564 trip days. All of the gear-specific αs are statistically significant. Most importantly, using the backward selection model, all eight coefficients are significantly less than 1 (*t* statistics, 404, 425, 355, 193, 65, 40, 50, and 28 with corresponding *p* values all < 0.0001). This means that any effort reduction resulting from a policy change would increase CPUE even in the absence of a causal effect on fishable biomass. These results provide strong evidence that drawing causal inferences about the effectiveness of marine reserves for fisheries management from fishery-dependent CPUE data is flawed.

The zone-specific effects are important (Table 1). Zone-specific constants are jointly significant ($F_{[12,404\,564]} = 13.90$, *p* value < 0.001), and zone-specific trends are jointly significant ($F_{[13,404\,564]} = 120.69$, *p* value < 0.001). Trends in individual zones varied, with some exhibiting positive trends and others, negative trends. In zones 6 and 8, where the reserves are located, trends are negative. Clearly, results omitting these trends would understate the benefits of reserves (or overstate the costs).

Zone–gear and zone–month interactions are also jointly significant, suggesting the need for multivariate regression models that control for interactions of harvest technology with spatial and temporal factors. Simple before–after comparisons are unlikely to provide unbiased estimates of reserve treatment effects because excluded covariates are unlikely to be orthogonal to the included ones. In simple before–after comparisons, there is no way to control for fishing effort and oceanographic conditions outside of the reserve.

The snapper variables are all positive and significant. When the snapper season is open, conditional catch of reef fish overall increases. This is not surprising for two reasons. First, for boats without a snapper permit, there is potentially less fleet competition for the other reef species. Second, for boats with a snapper permit, there is one less constraint. Catch would thus increase as long as substitute target species are not easier to catch. The positive effect of the class 1 dummy simply suggests that, on average, these vessels catch more than the rest of the fleet. Positive interaction terms mean that this margin over the rest of the fleet is larger during snapper season.

To quantify announcement effects and treatment effects, it is necessary to evaluate the estimates in Table 1 at the relevant time indices. We use the parameters from the backwards-selection model. The instantaneous net announcement effect is zero, whereas the trend is positive. After 1 year, the net effect is a 19% increase in conditional catch. Because the reserve was not yet established, the upward trend cannot be attributed to the reserve itself. Whether or not fishing vessels anticipated the formation of reserves by adjusting their behavior is difficult to answer because it ultimately requires information about perceptions that is not in the logbook data. It may be possible to explore this issue further in a survey. Biologically, the upward trend may be attributable to the arrival of a strong recruitment class that temporally coincides with the reserve announcement and spatially coincides with the reserve zones. It is impossible to test this hypothesis with fishery-dependent data.

Quantifying the net treatment effect requires evaluating the treatment estimates at particular time indices but also requires a temporal baseline. We chose the last day of the announcement period as the relevant baseline. Thus, the instantaneous effect (in logs) of treatment is $(\phi_1 + \phi_2 T) - (\mu_1 + \mu_2(T - 1))$. The resulting instantaneous effect is a 4% decrease in conditional catch. This seems plausible given that the two marine reserves, while closing off only a small percentage of the fishing zones, represent prime habitat for certain reef species.

By the end of October 2004, the net treatment effect was –14% in reef-fish catch, declining over the time since the reserve went into effect. The reason for the negative trend inferred by reserves is not immediately intuitive. If we attach a purely biological interpretation, then it appears that reserves

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Table 1. Fixed effects regressions.

	Full model				Backwards-selection model			
	Parameter estimate	Standard error	*t* statistic	*p* value	Parameter estimate	Standard error	*F* statistic	*p* value
Announcement shift	−1.12965	0.22047	−5.12	<0.0001	−1.12393	0.22043	26.00	<0.0001
Announcement trend	0.00047693	0.00008665	5.50	<0.0001	0.0004754	0.00008662	30.12	<0.0001
Reserve instantaneous effect	0.33688	0.04008	8.41	<0.0001	0.337	0.02559	173.36	<0.0001
Reserve trend effect	−0.00007532	0.00001273	−5.92	<0.0001	−0.0000743	0.00000832	79.78	<0.0001
Postreserve common shift	0.00262	0.03146	0.08	0.9336		Not significant		
Postreserve common trend	0.00001973	0.00000985	2.00	0.0452	0.00002037	0.00000272	56.20	<0.0001
Month before starting in 2001	0.02399	0.0094	2.55	0.0107	0.02366	0.00936	6.38	0.0115
Grouper closure period	0.08118	0.01267	6.41	<0.0001	0.08103	0.01261	41.29	<0.0001
Month after starting in 2001	−0.01588	0.00921	−1.72	0.0848	−0.01556	0.00917	2.88	0.0897
Snapper open period	0.03516	0.00414	8.50	<0.0001	0.03515	0.00411	73.23	<0.0001
Class 1	0.26757	0.01442	18.56	<0.0001	0.26745	0.0144	344.91	<0.0001
Class 1 × snapper open	0.10089	0.01866	5.41	<0.0001	0.10215	0.01861	30.13	<0.0001
Number of vessels	0.00928	0.00024398	38.02	<0.0001	0.00929	0.00024282	1463.31	<0.0001
Crew number	0.02493	0.00166	15.06	<0.0001	0.02497	0.00165	227.67	<0.0001
Alpha_gear1	0.02556	0.00242	10.57	<0.0001	0.0255	0.00241	111.49	<0.0001
Alpha_gear2	0.15814	0.00205	77.05	<0.0001	0.15779	0.00198	6361.85	<0.0001
Alpha_gear3	0.34608	0.00186	186.30	<0.0001	0.34625	0.00184	35316.10	<0.0001
Alpha_gear4	0.33602	0.00357	94.13	<0.0001	0.33656	0.00344	9555.31	<0.0001
Alpha_gear5	0.57417	0.00705	81.43	<0.0001	0.577	0.00652	7826.06	<0.0001
Alpha_gear6	0.14012	0.02163	6.48	<0.0001	0.13797	0.02145	41.39	<0.0001
Alpha_gear7	0.53519	0.01003	53.36	<0.0001	0.5316	0.00932	3256.07	<0.0001
Alpha_gear8	0.25759	0.03837	6.71	<0.0001	0.24783	0.02684	85.29	<0.0001
Area_constant_1	−0.07279	0.23525	−0.31	0.757		Not significant		
Area_constant_2	1.1115	0.22255	4.99	<0.0001	0.88867	0.03388	688.05	<0.0001
Area_constant_3	0.70739	0.26163	2.70	0.0069	0.6592	0.03595	336.23	<0.0001
Area_constant_4	2.50875	0.32923	7.62	<0.0001	2.28874	0.05695	1615.36	<0.0001
Area_constant_5	1.28692	0.20171	6.38	<0.0001	1.30026	0.11626	125.09	<0.0001
Area_constant_6	1.02204	0.16757	6.10	<0.0001	1.03754	0.03312	981.38	<0.0001
Area_constant_7	1.52062	0.23538	6.46	<0.0001	1.50972	0.15981	89.25	<0.0001
Area_constant_8	0.07875	0.55888	0.14	0.8879	0.11346	0.0398	8.13	0.0044
Area_constant_9	0.28447	0.20833	1.37	0.1721	0.26185	0.04365	35.99	<0.0001
Area_constant_10	0.34602	0.18158	1.91	0.0567	0.4835	0.02403	404.75	<0.0001
Area_constant_11	0.83074	0.15393	5.40	<0.0001	0.81904	0.04402	346.16	<0.0001
Area_constant_12	−1.40726	0.36933	−3.81	0.0001	−0.69245	0.0719	92.75	<0.0001
Area_constant_13		Restricted for identification				Restricted for identification		
Area_trend_1	0.00001031	0.00000672	1.53	0.1249	0.00001104	0.0000064	2.97	0.0846
Area_trend_2	−0.00001846	0.00000631	−2.92	0.0034	−0.00001876	0.0000062	9.14	0.0025
Area_trend_3	0.0000953	0.00000766	12.44	<0.0001	0.00009541	0.00000759	157.90	<0.0001
Area_trend_4	0.00003339	0.00000651	5.13	<0.0001	0.00003348	0.00000646	26.89	<0.0001
Area_trend_5	0.00000305	0.00000525	0.58	0.5612		Not significant		
Area_trend_6	−0.00003304	0.00000484	−6.83	<0.0001	−0.00003435	0.0000043	63.87	<0.0001
Area_trend_7	−0.000086	0.00000543	−15.84	<0.0001	−0.00008725	0.00000501	303.25	<0.0001
Area_trend_8	−0.00008624	0.000007	−12.31	<0.0001	−0.00008736	0.00000665	172.38	<0.0001
Area_trend_9	−0.00018827	0.00000778	−24.21	<0.0001	−0.00018964	0.0000075	638.48	<0.0001
Area_trend_10	−0.0000506	0.00000696	−7.27	<0.0001	−0.00005037	0.00000691	53.14	<0.0001
Area_trend_11	−0.00002695	0.00000896	−3.01	0.0026	−0.00002679	0.00000892	9.03	0.0027
Area_trend_12	0.00018906	0.00001651	11.45	<0.0001	0.00019157	0.00001544	153.93	<0.0001
Area_trend_13	0.00012788	0.00000775	16.49	<0.0001	0.00012771	0.0000071	323.39	<0.0001
Monthly_dummy_1	−0.37276	0.21012	−1.77	0.076	−0.4119	0.03014	186.75	<0.0001
Monthly_dummy_2	0.0829	0.18867	0.44	0.6604		Not significant		
Monthly_dummy_3	−0.05645	7688.33495	0.00	1	−0.05931	0.02978	3.97	0.0464
Monthly_dummy_4	0.0431	4555.99963	0.00	1	0.05155	0.01205	18.31	<0.0001
Monthly_dummy_5	−0.81154	0.22869	−3.55	0.0004	−0.37297	0.0581	41.21	<0.0001
Monthly_dummy_6	0.18991	0.18757	1.01	0.3113	0.12925	0.03263	15.69	<0.0001
Monthly_dummy_7	0.47826	0.19575	2.44	0.0146	0.39394	0.0223	311.95	<0.0001

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Table 1 (*concluded*).

	Full model				Backwards-selection model			
	Parameter estimate	Standard error	*t* statistic	*p* value	Parameter estimate	Standard error	*F* statistic	*p* value
Monthly_dummy_8	0.33685	0.1928	1.75	0.0806	0.29855	0.03032	96.96	<0.0001
Monthly_dummy_9	0.11447	0.20371	0.56	0.5742	0.07087	0.03229	4.82	0.0282
Monthly_dummy_10	–0.06814	0.20734	–0.33	0.7424	–0.16204	0.04051	16.00	<0.0001
Monthly_dummy_11	–0.20152	0.19539	–1.03	0.3024	–0.16491	0.02421	46.40	<0.0001
Monthly_dummy_12	Restricted for identification				Restricted for identification			
79 gear–month interactions	Jointly significant $F_{[79,404\,564]} = 44.28$, p value < 0.0001				61 of 79 significant at 10% level or better			
75 gear–zone interactions	Jointly Significant $F_{[75,404\,564]} = 119.23$, p value < 0.0001				63 of 75 significant at 10% level or better			
132 month–zone interactions	Jointly significant $F_{[132,404\,564]} = 19.56$, p value < 0.0001				112 of 132 significant at 10% level or better			
Observations	404 564				404 564			

Note: The dependent variable is the natural logarithm of individual daily vessel catch. Trend variables are scaled based on the number of days from the beginning of the sample period.

cause declines in fish biomass available for capture, all else being equal (something we strongly doubt could be true). The most parsimonious explanation, however, is that the time frame of the study was sufficient to reveal a gradual dampening effect of lost fishing area but not long enough to reveal catch benefits. As a result, the net treatment effect is trending downward in-sample. This means that the adult spillover from the closed areas is not generating a net benefit to fisheries. This could change over time, once fish in the reserve generate offspring that enter the fishery. For instance, by the latter part of 2004, the cutoff time for this study, gag offspring generated during the first year of reserve protection (2000) would be just reaching the minimum size limit making them available to the fishery. Thus the negative trend we see now is based on recruitment of a single year class. As new data become available, these models can be rerun to examine whether this treatment effect changes over time.

Discussion

As we transition towards a holistic view of the marine environment and the services that it provides, it is essential to learn how spatially explicit management tools such as marine reserves function. However, before we can truly assess the performance of marine reserves, fisheries biologists, economists, and managers must be able to answer the following question: If marine reserves enhance fisheries yields, how would we know? In this paper, we shed some light on this question by illuminating the hidden assumptions in previous retrospective analyses. We show by example that these assumptions are unlikely to hold where management includes marine reserves for large-scale fisheries management. Our results suggest proceeding cautiously with interpreting retrospective analyses that do not control for curvature in fishing production technologies, coexistence of multiple policy layers, heterogeneity across vessels, space, and time, and perhaps, most importantly, selection effects of fishing vessels in treatment and reference groups.

To move towards retrospective analyses that more convincingly draw causal inference, we propose a vessel-based standard for judging the fishery effects of marine reserves. The effectiveness of a marine reserve can only be assessed relative to a valid counterfactual case that is most reasonably defined at the level of individual fishing vessels. We illustrate an empirical method for constructing that counterfactual case. Unless the same people with the same vessels are fishing at the same level of intensity before and after forming a reserve in the reference sites, the search for BACIP is futile. Instead, fisheries researchers should use fishery-independent information on BACIP to inform the design of retrospective analyses like the one that we present.

Our approach in this paper is part of an emerging literature on program evaluation of environmental policy. This literature seeks to isolate policy effects on economic metrics, as well as on physical environmental outputs using nonexperimental data. For example, Gray and Shadebegian (2003) analyze the effects of environmental regulations on plant-level productivity and show that controlling for plant-level technological differences is essential to quantifying the effects of regulations. Strikingly, Greenstone (2004) analyzes US sulfur dioxide emissions, which have declined 80% since the 1970s, and finds that the Clean Air Act was not the cause of this large decline.

Existing retrospective analyses of the effects of reserves on fisheries (McClanahan and Kaunda-Arara 1995; Roberts et al. 2001; Russ et al. 2004) do not address key issues for isolating policy effects that are standard in the program evaluation literature and instead make simplifying assumptions. These analyses neither condition on individual skill and technology differences of harvesters nor directly address the counterfactual case that we outline above, raising questions of internal validity (i.e., whether the treatment effects are measured correctly). By using CPUE as an indicator of the policy impact, they also embed an implicit assumption about the fishing production function in the analysis that may or may not be valid. Roberts et al. (2001), for instance, show that 5 years after reserve placement there is a statistically significant increase in CPUE for artisanal reef fishermen in

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St. Lucia. However, without a reference site, it is not clear that the increase in CPUE can be attributed to the reserve treatment (Hilborn 2002). Suppose, for example, that an environmentally induced increase in recruitment coincided with establishment of the reserve. In this hypothetical situation, inferences about the effects of marine reserves on adjacent fisheries simply confound correlation with causation. In a long-term study of the Apo Island marine reserve, Russ et al. (2004) attempt to address the need for reference sites by comparing CPUE in a reserve before and 16–19 years after establishment with CPUE in reference areas *near* and *far* from the reserve. Are there hidden assumptions in this approach? Suppose that after reserve formation, highly skilled fishermen are disproportionately attracted to the reserve boundary and fish in close proximity to the reserve. If this occurs, drawing inferences about the reserve effectiveness from CPUE changes suffers from selection bias. Measured changes in CPUE are at least partly attributable to the fleet behavior. Thus, isolating the true policy impact requires controlling for selection.

Even if there are no selection effects and the modeling assumptions are internally valid, we are faced with the question of whether these results generalize to commercial reef fisheries on the scale practiced in the United States. Homogenous gear, for example, might be a reasonable assumption for small-scale artisanal fisheries. However, large-scale commercial fisheries generally involve heterogeneity in gear choices (Eggert and Tveteras 2004), spatial decision-making (Abrahams and Healey 1990; Mistiaen and Strand 2000; Smith 2005), and captain skill (Abrahams and Healey 1990; Pascoe and Coglan 2002). Without controlling for these factors, there are also reasons to doubt the external validity of existing retrospective studies. As such, we propose a more general model that nests existing studies, allows for differences across fishing production technologies, includes a range of spatial, temporal, and individual heterogeneity, and controls for selection effects.

Though we focus on fishery impacts, our results also question whether we can measure the pure biological effects of reserves without taking a program evaluation approach. Murawski et al. (2000) take an experimental approach to examine the impact of large-scale closed areas on the scallop fishery in the Northeast Atlantic using fishery-independent data. They find that biomass increases both within and outside the closed areas, and the relative increase is higher within the reserve. Though these authors acknowledge the importance of displaced fishing effort, the relative increase in biomass within and outside a reserve is a function of fishing effort outside the reserve, and this effort implicitly is not controlled for in the comparison. We submit that statistically controlling for effort outside a reserve is essential for measuring biological effects within a reserve because assessing these effects is based on before–after comparisons between the reserve and outside areas. Program evaluation offers a promising approach to deal with these situations.

For our particular application, we do not yet have a definitive answer on whether the two reserves that we study benefit fisheries. Because of life history characteristics of groupers and other reef-fish species, we are reasonably certain that the reserves have not been in place long enough for all of the potential benefits to materialize. We have less certainty about the spatial scope of reserve effects outside the reserve boundaries. Our assumption that reserve effects will manifest in the surrounding NMFS statistical zones posits a reasonably large spatial scope, especially for adult spillover, but it is plausible that larval export effects of reserves are not fully contained in the NMFS statistical zones where the reserves are located. It may be that some larger subset or even the entire fishery is treated if larvae from the reserve are distributed over very large areas. If this is the case, the treatment effect is in ϕ_1, ϕ_2, μ_1, and μ_2, and isolating it from coincident changes in the fishery is not possible. This will always pose challenges for evaluating the effectiveness of marine reserves. Fisheries scientists cannot simultaneously measure the spatial scope of reserve spillovers and evaluate the effects of reserves on catch. Either one imposes a spatial scope and tests effectiveness, or one imposes a level of effectiveness and tests for a spatial scope. We argue that fishery-independent data should be used to determine spatial scope of spillovers, and fishery-dependent data can be reserved for testing effectiveness. Ongoing tagging studies will ultimately help to evaluate our assumption about treatment zones in the future. Other applications of our technique are likely to be fruitful if reserves have been in place longer and there is more fishery-independent information on larval transport. This may be the case for large-scale reserves in the Northeast Atlantic.

Another plausible explanation of the negative trend in catch is that the stock is trending downward because of the bioeconomic cycling from open access (Wilen 1976; Bjorndal and Conrad 1987), and we simply have not observed the reserve for long enough to see the upward trend. This is consistent with a concentration of fishing pressure along the edge of each reserve, a phenomenon documented for fishing vessels in the Northwest Atlantic (Holland 2004) and seen by one of us (F.C. Coleman) around the Madison–Swanson Reserve.

Our approach has many advantages over existing retrospective analyses of fishery-dependent data. We control for gear differences, effort changes, environmental trends, and selection effects that left uncontrolled could lead to spurious conclusions about the effectiveness of marine reserves. If catch is the product of stock and effort, effort near and far from the reserve is unchanged before and after the policy, there are no environmental changes from before to after reserve formation, and individual fishing vessels are homogenous, then our approach based on individual catches aggregates to overall catches. In this sense, our approach nests that of Russ et al. (2004).

Nevertheless, our approach has important limitations. Beyond the issue of spatial scope of reserve effects discussed above, we do not control for catch composition after formation of the reserve (neither do previous studies). Vessels may substitute across low- and high-valued species within the reef-fish complex. Inability to control for this possibility partly reflects our data; separating effort on a species-by-species basis is problematic in multispecies fisheries. An interesting extension would be to explore the reserve treatment effect through revenue functions rather than catch functions and explore whether the sign of the treatment effect is the

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same when defined in terms of revenue. Another limitation is that our trend variables and the number of vessels fishing in the zone, which capture aggregate effort, may imperfectly control for the dynamic effects of aggregate effort on stocks. This type of criticism could apply to any program evaluation in which there is a latent state variable and nonlinear dynamics. Indeed, within economics there is a tension between program evaluation and dynamic structural models to measure policy impacts. Still, it is essential to note that all of these limitations apply to previous retrospective analyses of marine reserve fishery impacts as well.

Naturally, estimation of a structural bioeconomic model provides an alternative way to assess the performance of reserves after their formation. This approach would simultaneously estimate parameters of the biological system, behavioral parameters of the harvest sector, and the direct policy effects. In the absence of a structural model, the combination of biological and economic dynamics unfolding over space with latent state variables makes it difficult to interpret the results of before–after analyses, even if they incorporate all of the controls that we suggest. In other words, we cannot disentangle the structural determinants of the treatment effect. Empirical bioeconomic models that are dynamic and spatially explicit in theory can overcome these challenges. In practice, they present enormous estimation challenges. These models are currently still in their infancy and will require considerable intellectual attention to be broadly useful in evaluating fisheries policy in the future.

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Chutes and ladders and other games we play with rivers. I. Simulated effects of upstream passage on white sturgeon

Henriette I. Jager

Abstract: River fragmentation by dams has often preceded declines in sturgeon populations, which suggests that reconnecting populations would contribute to their recovery. This study used a population viability model to quantify the effects of upstream passage at dams on white sturgeon (*Acipenser transmontanus*) metapopulations inhabiting a series of long (source) and short (sink) river segments. Simulated river systems with high interspersion of long and short segments and a long segment far upstream supported the healthiest metapopulations, suggesting biological criteria for siting dams. Contrary to expectation, the model predicted that upstream passage, without screening or downstream passage, was harmful to the metapopulation as a whole. However, upstream passage was beneficial when downstream migration was either restricted (by screening larger fish) or made safe (by providing downstream passage). The combination of upstream and downstream passage was most beneficial at dams above a long river segment. Screening, alone or combined with upstream passage, was most beneficial at dams below a long segment. These theoretical results highlight the need for field research to evaluate management options and provide practical guidance for restoring sturgeon metapopulations in large rivers.

Résumé : La fragmentation des rivières par les barrages précède souvent le déclin des populations d'esturgeons, ce qui laisse croire qu'un rétablissement des connexions entre les populations pourrait contribuer à leur restauration. Un modèle de viabilité de la population permet ici de quantifier les effets des passages vers l'amont dans les barrages sur les métapopulations d'esturgeons blancs (*Acipenser transmontanus*) qui habitent dans des segments longs (sources) et courts (pertes) de rivière. Les systèmes de rivière simulés, à forte alternance de segments longs et courts, qui possèdent un long segment dans la partie amont tout à fait supérieure contiennent les métapopulations les plus saines, ce qui indique qu'il y a des critères biologiques pour le positionnement des barrages. Contrairement aux attentes, le modèle prédit qu'un passage vers l'amont, sans triage ni passage vers l'aval, est désavantageux pour la métapopulation dans son ensemble. Cependant, le passage vers l'amont est bénéfique lorsque la migration vers l'aval est restreinte (par la rétention des poissons plus grands) ou rendue plus sécuritaire (par l'établissement de passages vers l'aval). La combinaison des passages vers l'amont et vers l'aval présente le plus d'avantages dans les barrages situés en amont d'un long segment de rivière. Le tri, avec ou sans passage vers l'amont, présente le plus d'avantages dans les barrages situés en aval d'un long segment de rivière. Ces résultats théoriques démontrent la nécessité de faire des études sur le terrain pour évaluer les options de gestion et ils permettent d'élaborer des recommandations pratiques pour la restauration des métapopulations d'esturgeons dans les grandes rivières.

[Traduit par la Rédaction]

Introduction

The landscape of rivers and streams has changed considerably over the past 200 years. Water flow is now stored behind reservoirs at over 75 000 dams that impound nearly all medium and large rivers in the continental USA (Graf 1999). Dams provide the flexibility to use water when it is needed for irrigation, electricity, and other purposes, but have ecological costs. Impoundment has diminished waterfalls, rapids, and floodplain wetland habitat in rivers (Dynesius and Nilsson 1994). Dams act as semipermeable barriers that bias migration patterns between fish populations by curtailing safe downstream migration of fishes while preventing upstream migration entirely.

Sturgeon species are uniquely adapted to diverse and dynamic large mainstem rivers, ranging widely to take advantage of scattered and seasonally abundant resources (Beamesderfer and Farr 1997). Habitat fragmentation by dams is considered responsible for declines in sturgeon populations by blocking movements and creating homogeneous reservoirs that reduce habitat diversity (Beamesderfer and Farr 1997). Because of their large size, downstream migration past dams is a particularly hazardous undertaking for sturgeons, and upstream movement past dams is impossible without special provisions.

This leads us to conclude that sturgeon populations should benefit from reconnection. In theory, populations in linked river segments are more likely to recolonize their neighbors after local extirpation, an event more common in short river

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segments fragmented by dams. Reconnection should also increase the likelihood that habitat requirements of all life stages are met by the wider diversity of habitat types available among adjacent river segments.

Riverine populations now separated by dams can be reconnected either by providing upstream passage or by translocating fish captured in one segment to another. Upstream passage is usually accomplished by constructing fish ladders at the dams. Fish ladders are designed for surface-oriented anadromous species with strong swimming and leaping ability (e.g., salmon and shad; Cada and Sale 1993). Current fish ladder designs are less effective for bottom-oriented sturgeons, but sturgeon do occasionally use them (Warren and Beckman 1993). Fish elevators, which have been installed for sturgeon in Russia and Holyoke Dam on the Connecticut River, USA, are effective (Kynard 1998) but costly. Preliminary results with spiral loop fish ladders are promising for sturgeon (Kynard et al. 2003), particularly at smaller, low-head dams.

This research, which relies on simulation, was motivated in part by the lack of available field data on population-level effects of upstream passage. The assumption that upstream passage benefits the fish populations involved has not been adequately tested. Gehrke et al. (2002) suggest that multi-year studies are needed to test this assumption. Although hydropower licenses in the USA often require upstream passage facilities, particularly at dams that block migration of anadromous species, long-term monitoring has not been required (Cada and Sale 1993). The usual measure of success for upstream passage is simply that fish are observed using the passage facilities, and even this criterion has been difficult for sturgeons to meet (Knights et al. 2002).

This study uses a simulation approach to quantify the benefits of reconnecting river segments to a metapopulation of white sturgeon (*Acipenser transmontanus*). Unassisted, voluntary upstream movements of white sturgeon are considered here, and a companion paper considers assisted movements (Jager 2006). Demographic effects of providing upstream passage are quantified, with and without mitigation efforts to reduce entrainment or the associated mortality. I simulate rivers composed of different configurations of long (source) and short (sink) segments to examine how river configuration influences the effectiveness of upstream passage.

The following questions are addressed: (*i*) What is the magnitude of costs and benefits of upstream passage to each population and to the metapopulation as a whole? (*ii*) Do costs and benefits to individual populations change depending on the length of the river segments above and below the dam? (*iii*) How do mitigation measures intended to reduce entrainment mortality influence results? Answers to these questions suggest practical guidelines for restoring sturgeons and fish species with similar ecology by providing upstream passage at selected dams.

Model description

I conducted simulation experiments with a population viability analysis (PVA) model designed to simulate the dynamics and future viability of white sturgeon populations. The simulation experiments described here compare populations simulated in a series of river systems with different configurations of long and short river segments. Simulated populations in long segments tend to increase (source habitat), and those in short segments tend to decrease (sink habitat). By comparing river configurations, the results of this study provide more general conclusions about situations that might benefit from reconnection.

The PVA model simulates the reproduction and mortality of individual white sturgeon inhabiting a series of adjacent river segments and migration between segments. It uses an annual time step and is driven by a Markov sequence of dry, normal, and wet years (see Jager et al. 2002, 2003). Because individual-based models are stochastic, I report the average and standard error of each response variable among replicate simulations.

Those aspects of the PVA model specific to this study are described below. Other aspects of the model are described in Appendix A. Model parameters and values used in these simulations are listed in Tables 1 and 2. Mortality factors simulated include baseline mortality, density-dependent mortality, temperature- and flow-related mortality during incubation, larval export, turbine strike, and hooking mortality.

River configurations

Pulliam (1988) introduced the distinction between source and sink habitat areas. Metapopulation theory suggests that source river segments support populations that recruit enough offspring to grow in size and export surplus individuals (Hanski and Gilpin 1991; Rieman and Dunham 2000). Populations in sink habitats do not produce a surplus; instead they decline when they are isolated from source habitats. River segments between closely spaced dams that consist of mostly reservoir habitat tend to be demographic sinks for sturgeons for a number of reasons. Short segments dominated by reservoir provide less spawning habitat for sturgeons (Beamesderfer and Farr 1997), and larvae that are produced are more likely to be swept into a downstream segment. I chose the lengths of river segments in the river such that long segments represent source habitats and short segments represent sink habitats.

Results from case studies produce results that may apply only to the particular river under study. Simulating a variety of different river configurations allows this study to draw more general conclusions about the effects of segment length and upstream–downstream position on the benefits of upstream passage because these two influences are not confounded. To initialize the model, I divide the total length of river, L_{tot} = 270 km, into a specified number of segments, N_s = 6, with three short segments (40 km) and three long segments (80 km). Twenty upstream–downstream configurations of these six segments (three long and three short) exist. All 20 combinations of short (sink) and long (source) segments shown in Fig. 1 are simulated.

Preliminary results suggested that trickle-down effects to the next adjacent segment could be important in determining the net benefit of reconnection. I therefore added a seventh short segment at the downstream end to minimize boundary effects. By including this extra segment, metapopulation indices account for trickle-down effects on the segment downstream.

Once the physical layout of river segments is established, the free-flowing length of river, L_{ff}, in each segment is esti-

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Table 1. Parameter values of the white sturgeon (*Acipenser transmontanus*) population viability model.

Parameter name	Parameter description	Reference	Baseline value
S_y	First year survival rate (year^{-1})	Calibrated	0.0002
S_j	Survival rate of juveniles (year^{-1})	Cochnauer 1983	0.855
S_a	Survival rate of adults (year^{-1})	Cochnauer 1983	0.855
t_{larva}	Duration (days) of demersal larval stage	Brannon et al. 1985	1.0
L_0, L_1	Free-flowing length (km) associated with 0% and 100%, respectively, chance of reaching reservoir	Calibrated	45, 12
$\bar{L}$	Average size at first maturity for females, males (cm)	Cochnauer 1983	156, 134
L_{SD}	Standard deviation of size at maturity for females, males (cm)	Cochnauer 1983	15, 15
A_{egg}, B_{egg}	Intercept and exponent, respectively, of relationship between fecundity (no. of eggs) and fork length (cm)	DeVore et al. 1995	0.072, 2.94
M_{down}	Maximum annual chance of attempting downstream migration (at high density)	K. Lepla*	0.05
K_{vb}	Rate of change in fork length (cm) with age (years)	Lepla and Chandler 1995	–0.045
T_0	Initial age (years)	Lepla and Chandler 1995	–0.795
L_∞	Maximum size (cm)	Lepla and Chandler 1995	275
D_{egg}	Optimal egg density (no.·km^{-1})	Calibrated	35
D_{opt}	Optimal adult density (no.·km^{-1})	Fixed	10.0
P_{sweep}	Maximum chance of export	Calibrated	0.6
S_{sweep}	Survival of larvae swept downstream	Fixed	0.1
H_{res}	Length (km) of reservoir assumed suitable for spawning	Fixed	1.0
B_{strike}	Slope of linear relationship between risk of turbine strike and fork length (cm)	Average for Snake River dams	0.0092
W_{screen}	Trashrack spacing (cm)	Average for Snake River dams	17.74

*Ken Lepla, Idaho Power Company, P.O. Box 70, Boise, Idaho 83707, USA, unpublished data.

Table 2. Parameter values and initial conditions listed below applied to all segments of the hypothetical rivers.

Parameter name	Parameter description	Dry years	Normal years	Wet years
$P_{entrain}$	Probability of entrainment	0.9956	0.9567	0.8322
S_{temp}	Age-0 temperature-related survival	0.8839	0.8574	0.8080

mated from a regression relationship with L_{tot}. Parameter values were estimated from segment length data for nine river segments in the Middle Snake River in the western USA (hereafter referred to as Snake River) ($R^2 = 0.98$) as follows:

$$(1) \qquad L_{ff} = 0.724\,L_{tot} - 9.486$$

According to this relationship, the short segments contain approximately 50% free-flowing habitat and 50% reservoir habitat, and the long segments contain approximately 60% free-flowing habitat and 40% reservoir habitat.

Several other site-specific parameters were needed (Tables 1 and 2). For parameters that would be expected to show neither a longitudinal trend nor a relationship to river segment length, I used average values from the Snake River segments. For parameters that might be expected to show such relationships, I developed empirical relationships based on data for the nine Snake River segments. In some cases, different values were used for wet, normal, and dry hydrologic years (Table 2). Temperature-related age-0 survival, S_{temp} (Appendix A) did not show trends with either distance downstream or segment length. Reservoir retention time, t_R, which influences survival of larval export, S_{larvae}, increased with reservoir length. I fitted a power relationship between t_R and reservoir length for each hydrologic year type (Fig. 2*a*; $R^2 = 0.90$ for all three). Average flow during spawning and incubation, Q_{spawn}, showed an increasing trend with distance downstream because of tributary inputs. I fitted a linear relationship (Fig. 2*b*) for each hydrologic year type ($0.82 \le R^2 \le 0.92$). Likewise, Q_{high}, the threshold flow above which flow is adequate for spawning, increased with distance downstream (Fig. 2*b*; $R^2 = 0.81$).

Simulation of downstream movement

Each year, simulated individuals ages 1 and older have an opportunity to move downstream. The probability that individual i will decide to move downstream, P_d, increases from zero to a maximum value of M_{down} at high densities, with an inflection point at the optimal white sturgeon density, D_{opt}. Let u_i be a random variate drawn for individual i from a uniform distribution on the interval [0,1] (i.e., $u_i \in U[0,1]$). The simulated fish decides to move if $u_i \le P_d$. The realized downstream migration rate is usually a smaller proportion of the population size than the individual probability because not all individuals succeed in moving downstream, as described below.

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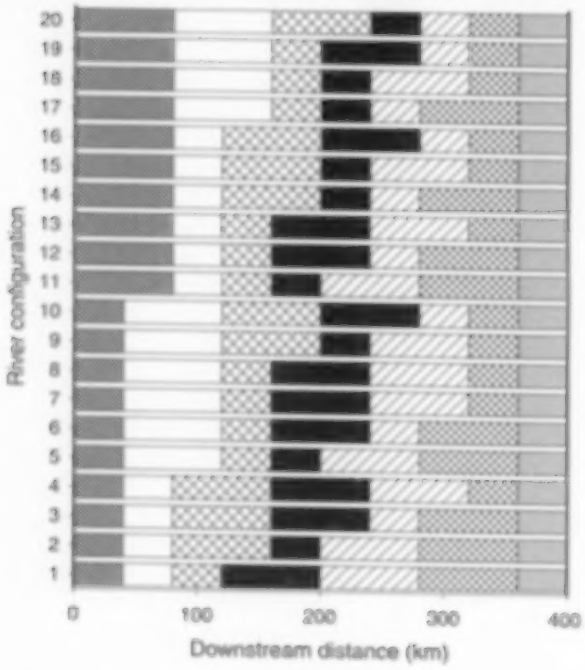
Fig. 1. Hypothetical river systems constructed of three long and three short segments, plus one short segment at the bottom. Twenty possible combinations of long and short segments are shown.

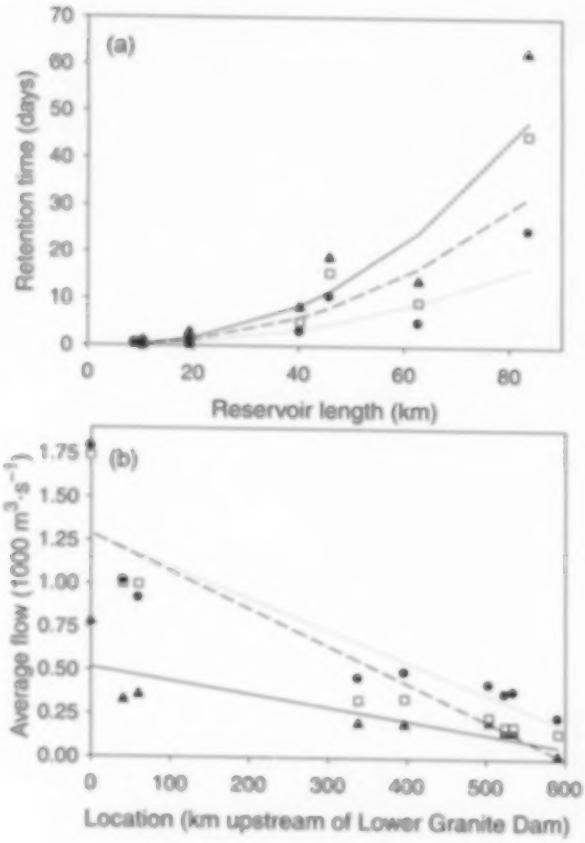


Once a particular individual chooses to move downstream, it is either entrained through the turbines or spilled over the dam. The model assumes that the probability of moving downstream with spilled flow is equal to the proportion of flow spilled, P_{spill}. A particular fish i is spilled if $u_i \leq P_{spill}$, $u_i \in U[0,1]$. This common assumption that fish "go with the flow" overestimated entrainment rates for juvenile salmon into diversions of the Sacramento River (Hanson 2001), but it nevertheless represents the best guess in the absence of data for white sturgeon. P_{spill} is higher in wet hydrologic years because flows exceed the capacity of the turbines more often. Simulated individuals that pass over the dam in spilled flow avoid any risk of mortality during downstream movement.

White sturgeon can avoid entrainment and the risk of turbine mortality if either a screening device or a downstream fish passage device is in place. The most common screening devices are racks with bars set at a fixed spacing to exclude large objects that might damage the turbines (Cada and Sale 1993). Screening reduces the downstream migration rate by preventing larger fish from moving downstream, except during high flows when water spills over the dam.

The model simulates screening by setting a screening width, W_{screen}, which is multiplied by proportion P_{screen} (Table 1). First, the model determines whether the fish is small enough to pass through the screen, a decision represented by an indicator function, $I_{entrained}$ (eq. 2). The white sturgeon remains in the upstream segment if its diameter exceeds the screening width (the model does not currently represent the risk of impingement against screening devices). The diameter of cylindrical fish i, W_i, is calculated as $(0.2765\ L^{1.07})/\pi$, with parameter values relating diameter to fork length, L, estimated from white sturgeon collected in the Snake River (K. Lepla, ID Power Company, P.O. Box 70, Boise, Idaho 83707, USA, unpublished data).

Fig. 2. Relationships from segments in the Middle Snake River used to parameterize hypothetical river configurations. (*a*) Power relationships for each hydrologic year type fitted between reservoir retention time, t_R, and reservoir length in the Middle Snake River ($R^2 = 0.90$ for all three). (*b*) Linear relationships for each hydrologic year type between average flow, Q_{space} (1000 $m^3 \cdot s^{-1}$), and distance upstream ($0.82 \leq R^2 \leq 0.92$) for dry years (circles, dotted lines), normal years (squares, broken lines), and wet years (triangles, solid lines).



$$I_{entrained} = \begin{cases} 1, & W_i \leq W \cdot P_{screen} \\ 0, & \text{otherwise} \end{cases} \quad (2)$$

Fish using downstream passage facilities, such as bypass channels, are able to migrate downstream safely by avoiding the turbines. To simulate downstream passage, the model permits white sturgeon to migrate to the segment downstream without excluding larger sizes and without risk of turbine mortality. Downstream passage, as simulated here, is probably safer than it is in reality because smaller juveniles

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following this alternative route might encounter higher-than-usual predation risk.

Three equations summarize the decision process above for individuals in river segment j. Equation 3 describes individual i's chance of downstream movement in year t, and eq. 4 describes the corresponding binomial decision to move or not to move downstream. The number of downstream migrants in year t is given by eq. 5, where $N_j(t)$ is the number of age-1 and older white sturgeon in river segment j at the start of year t.

$$(3)\quad P_{\text{down},j}(t) = \begin{cases} P_d, & \text{with downstream passage} \\ P_d[P_{\text{spill}}(t) + [1 - P_{\text{spill}}(t)]I_{i\in\text{entrained}}], & \text{otherwise} \end{cases}$$

$$(4)\quad I_{i\in\text{down}} = \begin{cases} 1, & \text{if } u_i \le P_{\text{down},j},\ u_i \in U[0,1] \\ 0, & \text{otherwise} \end{cases}$$

$$(5)\quad \text{Migrants}(t) = \sum_{i=1}^{N_j(t)} I_{i\in\text{down}}$$

In three sets of simulation experiments, I compared three options for downstream movement past the dam with upstream passage. The first scenario simulated migration using wider screens at the dam. The screen spacing was set to the average for dams in the Snake River, which excluded white sturgeon with fork lengths greater than 143 cm. In the second scenario, this spacing was halved (narrow spacing scenario), but only at the dam with upstream passage. In the third scenario, I simulated downstream passage again, but only at the dam with upstream passage.

Entrainment mortality

Given that an individual white sturgeon has been entrained, its likelihood of being killed by turbine blade strike depends on the fish's length and the type of turbine (Fig. 3). The model estimates the risk at each dam using two parameters: (*i*) B_{strike}, the slope of a linear relationship between strike probability and sturgeon size and (*ii*) W_{screen}, the size of the largest fish that can pass through the downstream screening device (Table 1). If the fish survives passage through the turbines, it moves to the downstream segment.

Simulation of upstream passage

In baseline simulations, migration probabilities are zero for nonadjacent segments and upstream segments. Voluntary upstream passage is simulated in scenarios with upstream passage using an individual probability of upstream movement equal to the maximum downstream probability, with no bias in ages or sizes of white sturgeon moving (i.e., strictly in proportion to abundance).

Preliminary simulations

Source–sink dynamics

To assess which segments were sources or sinks, I compared population dynamics in simulations of populations in river configuration 15, with and without downstream migration. Results were similar for other river configurations. When the segments were isolated (Fig. 4*a*), populations in long segments increased and the populations in short segments declined, usually reaching extinction within a 300-year time span. When simulating downstream migration (Fig. 4*b*), populations in long river segments attained stable sizes (usually greater than 500 individuals). Thus, the three short segments acted as demographic sinks. The long segments acted as demographic sources, which, if situated upstream of a short segments, may subsidize short segments through downstream migration.

Effects of river configuration

In baseline simulations (no upstream passage and wide screening), populations in the long segments were larger at the end of the simulation than populations in short segments. Among the 20 river configurations, configurations with a long segment positioned farther upstream and with high interspersion of long and short segments had a higher metapopulation status, as measured by NT_{500} (the sum of final population sizes including all seven populations, where the maximum counted in any population is 500), at the end of the simulations (Fig. 5).

Effects of screening width

To understand the effects of screening smaller and smaller fishes, a series of simulations varied the screening widths at the dam below segment two. The screening width was reduced by multiplying the wider screening width by a fraction, P_{screen}. This series compared results for P_{screen} values of 0.0, 0.2, 0.4, 0.6, 0.8, and 1 for river configuration 15 (see Fig. 1). The case of 0.0, although unrealistic, was included to simulate the limiting case of no downstream migration. The results presented are final population sizes below and above the dam and cumulative values including emigration from above the dam, immigration below the dam, and turbine mortality.

Decreasing the size of fish able to pass through the screen increased the size of the final population simulated above the dam (open circles in Fig. 6) and decreased turbine mortality (hatched bars in Fig. 6) as expected. Interestingly, the downstream population reached the largest size at an intermediate width because very close spacing reduced immigration of juveniles from the upstream population (closed circles in Fig. 6). The narrow screening scenario (50% of wide screening) increased the size of the population above the dam in 99% of cases and increased the population below the dam in 94% of cases (river configurations and dams).

Passage simulations

Because individual-based models are stochastic, 30 replicate metapopulations are simulated for 300 years. The average and standard error (SE) over 30 replicates is presented for NT_{500}. NT_{500} is the sum of final population sizes including all seven populations, where the maximum counted in any population is 500. This makes the index more sensitive to increases in small population and less sensitive to increases in populations that are already large. Six scenarios simulated are as follows: (*i*) baseline: wide screening alone, (*ii*) narrow screening alone, (*iii*) downstream passage alone, (*iv*) upstream passage with wide screening, (*v*) upstream pas-

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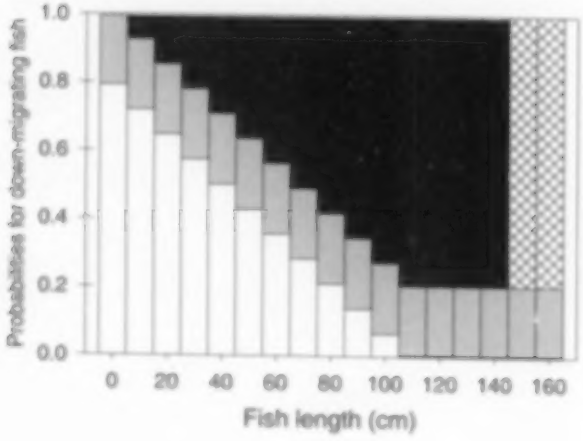
Fig. 3. Simulated probabilities of four possible outcomes for individual white sturgeon (*Acipenser transmontanus*) selected to attempt downstream migration during a wet year: sturgeon remains upstream (crosshatch), survives spilling over the dam (shaded), survives entrainment (open), or is struck by a turbine during entrainment (solid). Sturgeon length influences whether an individual is entrained and, if so, its risk of being struck by turbine blades.



sage with narrow screening, and (*vi*) upstream passage with downstream passage. Below, the three options without upstream passage are described in one section and the three corresponding options with upstream passage are described in the following section.

No upstream passage with three options for downstream movement

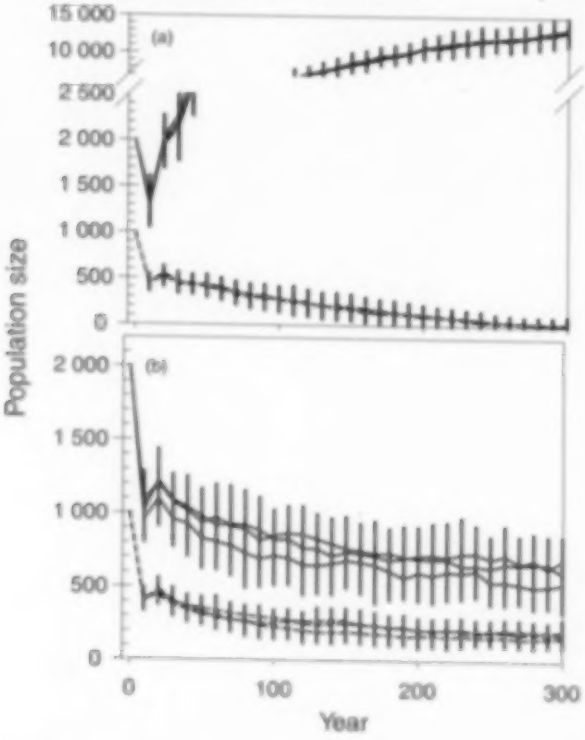
For each river configuration, simulations without upstream passage were run for each of three options for downstream movement: (*i*) wide screening, (*ii*) narrow screening, and (*iii*) downstream passage. There was only one simulation for the baseline scenario with no upstream passage and wide screening at all dams. In contrast, there were six simulations each for narrow screening and downstream passage because these options were applied at each dam, one at a time (the other dams have wide screening). Results from these scenarios were used to separate the effects of upstream passage from the mitigation simulated for downstream movement.

Upstream passage with three options for downstream movement

To evaluate the costs or benefits of providing upstream passage, I simulated upstream passage at each of six dams in each river configuration. These simulations assumed wide screening at all dams. In addition, I simulated upstream passage combined with two different options for reducing turbine mortality only at the dam with upstream passage: narrow screening and downstream passage. These three options were described earlier in the section on Simulation of downstream movement.

First, I present individual population results above and below one dam in a particular configuration to illustrate the effects of upstream passage within river configurations. Next, I present patterns in metapopulation responses as a function of

Fig. 4. Long-term simulations of configuration 15 compare the fates of long (upper, solid lines) and short (lower, broken lines) river segments (*a*) when they are isolated and (*b*) when they are connected by downstream migration. Lines connect the mean population size predicted by 30 replicate simulations. Error bars show the standard deviation of the predictions.



the length of the segments above or below the dam with upstream passage and the longitudinal position of the dam.

Results

Upstream passage with wide screening

Within-river configuration

Configuration 15 was used to illustrate the effects of upstream passage within a river. In general, simulating upstream passage at a dam resulted in higher final numbers in the population above the dam (compare solid bars in Figs. 7*b*–7*f* with shaded bars directly above in Fig. 7*a*) and smaller final numbers in the population below the dam (compare open bars in Figs. 7*b*–7*f* with Fig. 7*a*). In most cases, the net effect on the metapopulation was negative. The net demographic benefit of upstream passage was greater when provided at a dam below a long segment (Figs. 7*b*, 7*d*, 7*f*). In these cases, declines in the downstream population appeared to be offset by increased downstream migration from the larger upstream population.

Across-river configurations

This section addresses the question, "Under what conditions does reconnecting white sturgeon populations by upstream passage benefit the metapopulation?" Upstream

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Fig. 5. Metapopulation status, NT_{500}, is higher for simulated river configurations with high interspersion and a long segment upstream. The following linear relationship has adjusted R^2 = 0.72: NT_{500} = 1980 + 30.7·interspersion − 120.7·long position.

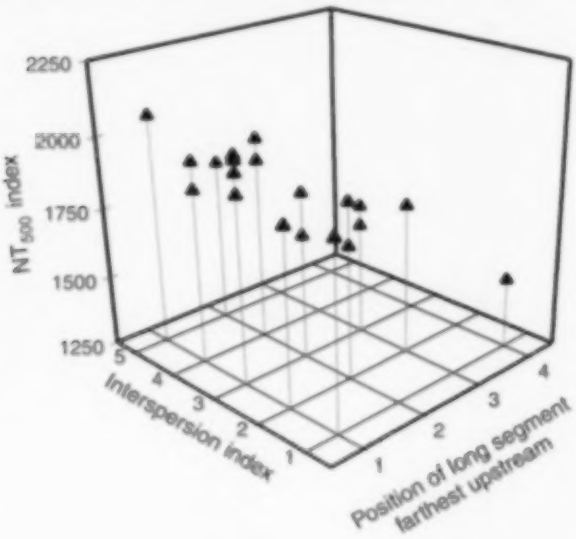
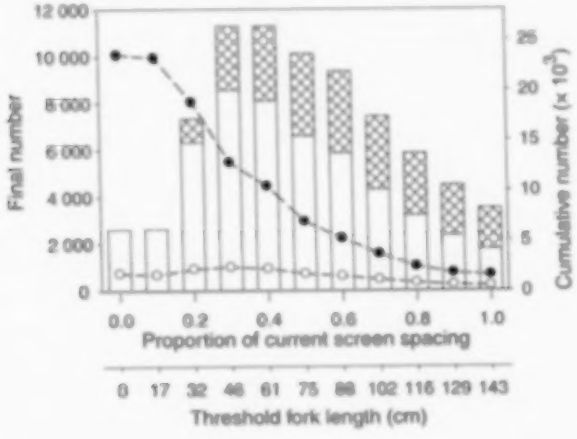
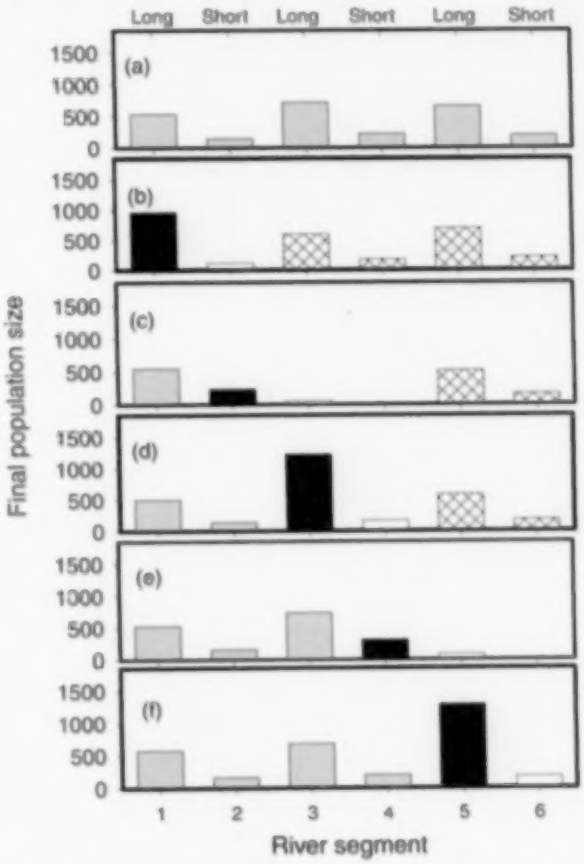


Fig. 6. Two lines show simulated final population sizes above dam (open circles) and below dam (solid circles) below segment two in configuration 15 in response to a proportional reduction in screening width. Stacked bars show cumulative (over time) immigration (open bars) and number of fish killed by turbine strike (crosshatched bars). The threshold fork length of sturgeon that can pass through the screen is indicated on the lower *x* axis.



passage increased the population above the dam in all but one of 120 cases (20 river configurations × 6 dams). Upstream passage decreased the population below the dam in 116 cases. In 94% of cases, the population two segments downstream of the dam also decreased in response to providing upstream passage. When averaged across all river configurations, simulated upstream passage had a negative

Fig. 7. Example of upstream passage for river configuration 15. The top graph (*a*) shows baseline results, where the *x* axis indicates the river segment (left is upstream) and the *y* axis indicates final population size in the segment. Panels *b*–*f* show the results of upstream passage at the dam below segment 1 (*b*), segment 2 (*c*), segment 3 (*d*), segment 4 (*e*), and segment 5 (*f*). In each graph, the solid bar is the upstream segment, the open bar is the segment immediately downstream, and other downstream segments are crosshatched. Shaded bars denote river segments not affected by passage.



demographic effect on metapopulations, as measured by NT_{500}.

As there were no cases of an appreciable increase in NT_{500} resulting from upstream passage, there was little point in exploring patterns in the index related to properties of the river configuration or of the dams involved in upstream passage. However, upstream passage was most detrimental when the downstream segment was long (compare solid bars in Fig. 8 with horizontal line), especially with a short upstream segment. In this case, white sturgeon inhabiting source habitats can move upstream into sink habitat.

Upstream passage combined with narrow screening

NT_{500} increased when narrow screening was simulated at dams that allowed upstream passage (Fig. 8). However, narrow screening at a given dam alone (i.e., without upstream

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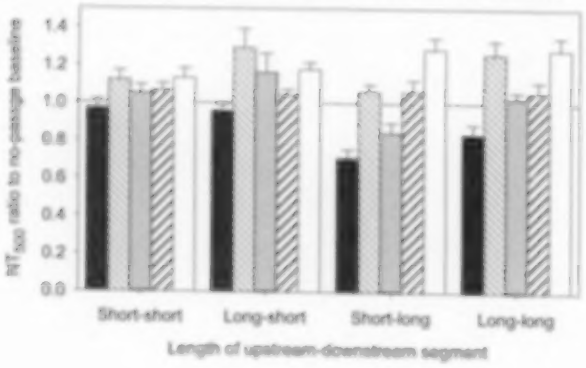
Fig. 8. Ratio of NT_{500} for each of five scenarios to NT_{500} for the baseline scenario (no passage and wide screening) for different combinations of long and short segments above and below the dam. The five scenarios are (*i*) upstream passage with wide screening (solid bars), (*ii*) narrow screening (narrow striped bars), (*iii*) upstream passage with narrow screening (shaded bars), (*iv*) downstream passage alone (wide striped bars), and (*v*) upstream and downstream passage (open bars). Scenarios with values above the horizontal line increased NT_{500} relative to the baseline and vice-versa. Error bars show one standard deviation.



passage at the dam) increased NT_{500} even more (open bars in Fig. 8).

Narrow screening was more beneficial without upstream passage because it had a positive effect downstream; as the upstream population grows, more small fish are exported downstream. Both upstream passage and narrow screening had a positive effect on the population upstream of the dam, but they had different effects on the population below the dam. Whereas upstream passage usually caused the final size of the population below the dam to decrease (116 of 120 cases), narrow screening usually caused an increase (113 cases). Trickle-down benefits were experienced two segments below the dam in 86% of cases with narrow screening alone, in 6% of cases with upstream passage only, and in 58% of cases with both.

I compared the ratio of NT_{500} for each treatment to that in the baseline situation for all combinations of long and short segments above and below the dam with upstream passage. This analysis suggests that upstream passage combined with narrow screening is harmful when the segment above the dam is short and the segment below the dam is long (Fig. 8). Narrow screening was more beneficial when the upstream segment was long (Fig. 8). The upstream–downstream position of the dam with passage did not have a significant effect on NT_{500} (minimum $p = 0.834$, $T = -1.009$, df = 18).

Upstream passage combined with downstream passage

Combining downstream and upstream passage at the same dam increased the average demographic status of metapopulations (open bars in Fig. 8). The simulated increase was greatest when the downstream segment was long. The demographic benefits of downstream passage were smaller without upstream passage (wide striped bars in Fig. 8). Average NT_{500} did not show a trend with the longitudinal position of the dam with passage.

As might be expected, downstream passage alone usually had the opposite effect of upstream passage; final population sizes usually decreased above the dam (94 cases) and increased below the dam (114 cases). When upstream passage was combined with downstream passage, all 120 cases showed an increase above the dam, but decreases below the dam occurred in only 27 cases. Trickle-down benefits were experienced two segments below the dam in 78% of cases. The trickle-down benefits for configuration 15 were substantially higher for upstream and downstream passage (Fig. 9) than for upstream passage alone (Fig. 7) when the upstream segment was long. For example, observe the increase in the simulated final population sizes of segments 2 and 3 in Fig. 9*b* compared with those of the same segments in Fig. 9*a* resulting from upstream passage at the first dam. Likewise, final populations increased in segments 5 and 6 (Fig. 9*d*) relative to baseline simulations (Fig. 9*a*), which was not evident in Fig. 7.

Discussion

Model predictions suggest that the status of white sturgeon metapopulations without upstream passage is higher in river configurations that have high interspersion of source and sink segments and a source segment far upstream. This implies that the configuration of dams can influence restoration efforts and that the siting of dams could be done in a way that better protects white sturgeon and similar species.

Simulation results for upstream passage differed from my initial expectations. Simulated efforts to reconnect populations by providing upstream passage alone did not augment the status of fragmented river metapopulation. To succeed with upstream reconnection, it was also necessary to simulate narrower screening or downstream passage at the dam with upstream passage.

Two scenarios that gave the best demographic results excelled under different circumstances. Both benefited simulated river metapopulations by providing positive effects downstream. Upstream passage combined with narrow screening increased metapopulation status in most cases. Narrow screening alone also benefited metapopulations, especially at dams between long upstream segments and short downstream segments.

Downstream passage was effective when combined with upstream passage. This scenario differs from that of a single river segment without a dam present only by the proportion of reservoir habitat. Passage in both directions was particularly beneficial for short upstream segments and long downstream segments.

The two scenarios (narrow screening alone and downstream with upstream passage) provided similar benefits for the remaining situations (both segments short or long). Both scenarios were more successful than upstream passage alone because they bolstered the combined populations, which in turn subsidized downstream segments.

This simulation study offers two take-home lessons. First, this study suggests that it is a good idea to monitor populations below the dam with passage to ensure that downstream demographic costs do not outweigh upstream benefits. Second, risks during downstream migration should be sufficiently low before providing upstream passage.

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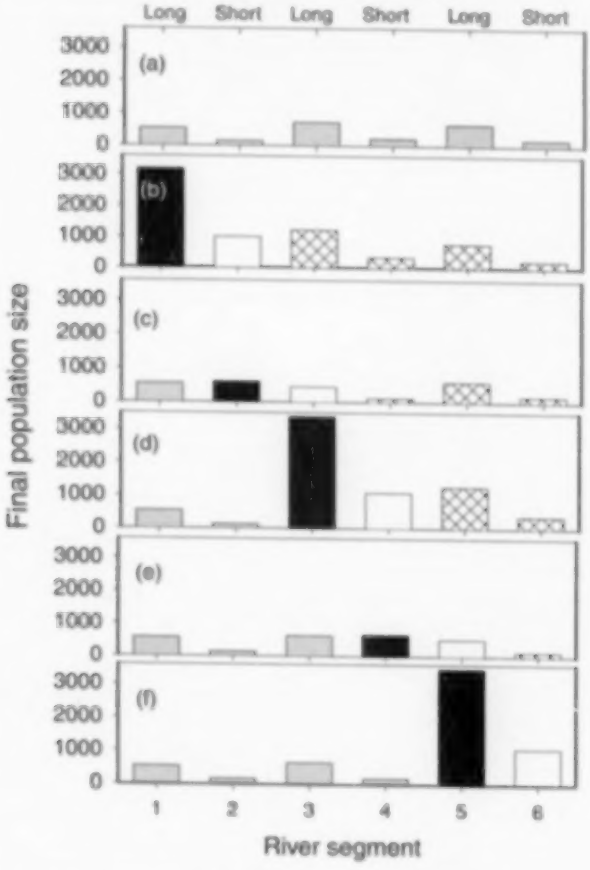
Fig. 9. Example of upstream passage combined with downstream passage for river configuration 15. The top graph (*a*) shows baseline results, where the *x* axis indicates the river segment (left is upstream) and the *y* axis indicates final population size in the segment. Panels *b–f* show the results of upstream passage at the dam below segment 1 (*b*), segment 2 (*c*), segment 3 (*d*), segment 4 (*e*), and segment 5 (*f*). In each graph, the solid bar is the upstream segment, the open bar is the segment immediately downstream, and other downstream segments are crosshatched. Shaded bars denote river segments not affected by passage.



As with any modeling study, these results depend on several model assumptions. First, this study applies to riverine fishes that require longer river segments and free-flowing habitat to reproduce. In rivers of the Pacific northwest, long river segments tend to support larger inland white sturgeon populations, but there are exceptions; a few large populations in the Lower Columbia River exist in short reservoirs that also provide access to the estuary. Results probably apply to other large-bodied fishes with life histories similar to that of the white sturgeon. For fish species that thrive in reservoir habitat, qualities other than segment length might distinguish source and sink habitat.

Second, sensitivity results suggest that the benefits of upstream passage decrease as density dependence becomes stronger. Because these simulations included a density-dependent spawning interval, the benefits of upstream passage could be higher if density dependence is weak. Third, decisions by fish to avail themselves of upstream passage in real-life situations might not match model assumptions about the number and sizes of fish that move upstream. One encouraging note is that simulated translocation experiments that moved fish upstream one segment produced similar results (Jager 2006), although the total number of white sturgeon moving upstream was higher for simulated upstream passage than for simulated translocation. As in this study, translocations to a recipient segment directly upstream of the donor were not usually beneficial, except for translocation combined with downstream passage (Jager 2006). Thus, model results were qualitatively similar in the two cases despite differences in the numbers of fish moved upstream. Other sensitivity results for this model are presented in Jager (2006).

If we wish to predict the effectiveness of mitigation measures at different dams, it is necessary to conduct regional-scale studies that include a sample of representative projects. Because we consider relicensing decisions in the USA on a case-by-case basis, monitoring requirements differ from one hydroelectric project to another. Monitoring to determine whether fish benefit from passage at the population level has been recommended (Cada and Sale 1993), but such studies have not been conducted. Ideally, regional-scale field research would be designed to obtain and provide consistent scientific guidance on the effectiveness of upstream passage in different situations. The results of this theoretical study provide testable hypotheses for future field studies to test and refine.

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Appendix A

The processes of reproduction, recruitment, and juvenile and adult survival are described below (see also Jager et al. 2001, 2002, 2003). Simulation of juvenile and adult movement was described earlier in the Model description section, along with other aspects of the model specifically relevant to simulating passage.

Initialization

Simulations were initialized with a density of 25 individuals >43 cm·km^{-1}. The initial size structure was 73% <95 cm, 22% between 95 and 171 cm, and 5% >171 cm.

Reproduction

The population viability analysis (PVA) model evaluates reproduction annually for each subpopulation. Each year, the model identifies the pool of adults eligible to spawn. Whether a particular individual belongs to this pool depends on its having reached maturity, its last spawning date, and its assigned rematuration interval. The onset of reproductive maturity is later for females than for males and is quite variable among individuals. The PVA model assigns each individual, i, a threshold length at maturity, Lc_i, at birth from a normal distribution with mean $\bar{L}$ and standard deviation L_{SD}, which are based on the length distribution observed among Snake River adults (Table 1). The indicator function in eq. A1 determines whether a white sturgeon has reached a mature size based on its current length, L_i.

$$\text{(A1)} \quad I_{i\,\text{mature}} = \begin{cases} 1, & L_i(t) \geq Lc_i \\ 0, & \text{otherwise} \end{cases}$$

The number of years between successive spawning events is also variable. An extended resting period between spawning events is a likely response to density-dependent limitation. Let $t_{\text{last},i}$ denote the last year that individual i spawned. In the model, the interval between spawning events increases when the density of adults is high enough to deplete food resources. Because white sturgeon do not show territorial social behavior and are often seen foraging with others, density-dependent effects are applied equally to all individuals. The spawning interval for females in river segment j increases with the density of adults $D_j(t)$, which is defined as the number with fork lengths longer than 170 cm divided by the length of free-flowing habitat in segment j plus a small length of reservoir habitat assumed to be suitable for spawning, H_{res} (Table 1). Female spawning interval rises from a minimum value, SI_{min}, at low densities to a maximum of SI_{max} at high densities, with a midpoint at optimal density D_{opt} (eq. A2).

$$\text{(A2)} \quad \text{SI}_j(t) = \text{SI}_{\text{min}} + \text{SI}_{\text{max}}\left(\frac{D_j^2}{D_{\text{opt}}^2 + D_j^2}\right)$$

Spawning aggregations in segment j include all individuals i eligible to spawn, where indicator function $I_{i\,\text{repe}}$ denotes the collection of individuals that are ready to spawn in year t, and t_{last} is the year this individual last spawned or first reached maturity (eq. A3).

$$\text{(A3)} \quad I_{i\,\text{repe}} = \begin{cases} 1, & t - t_{\text{last},i} \geq \text{SI}_j(t) \\ 0, & \text{otherwise} \end{cases}$$

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Each spawning female releases eggs, where the fecundity of female white sturgeon increases with female size (Cochnauer 1983). The model currently estimates fecundity of each female in two steps. Equation A4 estimates fork length, L_i, in centimetres from age in years, A_i, with Von Bertallanfy parameters (estimated by Lepla and Chandler (1995); Table 1). Fecundity, E_i, increases with fork length for females as shown in eq. A5 (DeVore et al. 1995).

$$L_i = L_\infty \{1 - \exp[K_{vb}(A_i + T_0)]\} \quad \text{(A4)}$$

$$E_i = \begin{cases} A_{egg} L_i^{B_{egg}}, & \text{female} \\ 0, & \text{male} \end{cases} \quad \text{(A5)}$$

The total pool of eggs spawned in a population of size N_j in segment j and year t is given by

$$\text{Total eggs}(t) = \sum_{i=1}^{N_j(t)} I_{i \in \text{mature}} \cdot I_{i \in \text{repr}} \cdot E_i \quad \text{(A6)}$$

If at least one male is ready to spawn, these eggs are fertilized and a male parent is assigned to eggs at random from the pool of spawning males.

Recruitment

The PVA model determines recruitment to age 1, $R(t+1)$, as the number of eggs that independently survive four sequential mortality risks during the first year of life: (*i*) natural mortality, S_y, (*ii*) density-dependent mortality, S_d, (*iii*) temperature-related mortality during incubation, S_{temp}, and (*iv*) larval export, S_{larva}:

$$R(t+1) = S_y \cdot S_d \cdot S_{temp} \cdot S_{larva} \cdot \text{Total eggs}(t) \quad \text{(A7)}$$

S_d increases from zero at zero egg density to one at an optimal egg density, D_{egg}. Values of S_{temp} listed in Table 2 are calculated for dry, normal, and wet hydrologic years.

Larval export can lead to substantial losses in shorter segments. The PVA model simulates larval export as follows. First, spawning is assumed to be in the free-flowing section, if there is one. The proportion of larvae that migrate is the product of the probability that a larva will reach the reservoir, P(reservoir), and the probability that a larva that has reached the reservoir will be swept downstream, P(swept|reservoir). The simulated probability that a larva enters the reservoir decreases exponentially as the length of free-flowing river, L_{fl}, increases. The probability of a larva being swept downstream once it is in the reservoir decreases as reservoir retention time, t_R, increases and as the duration of the demersal stage, t_{larva}, increases. The retention time of each reservoir differs for the three hydrologic year types (Fig. 2*a*). Equation A8 estimates the proportion of larvae moving downstream. Survival of larval export, S_{larva}, equals the fraction of total larvae not swept downstream.

$$S_{larva} = 1 - P\{\text{swept} \mid \text{reservoir}\} P\{\text{reservoir}\}$$

$$P\{\text{reservoir}\} = \begin{cases} 0, & L_{fl} \geq L_0 \\ \dfrac{(L_{fl} - L_0)}{(L_1 - L_0)}, & L_1 \leq L_{fl} \leq L_0 \\ P_{sweep}, & L_{fl} \leq L_1 \end{cases} \quad \text{(A8)}$$

$$P\{\text{swept} \mid \text{reservoir}\} = \begin{cases} \dfrac{t_{larva}}{t_R}, & t_{larva} \leq t_R \\ 1, & \text{otherwise} \end{cases}$$

If spawning aggregations are equally likely to occur anywhere in the free-flowing stretch, then the average upstream distance of spawning sites increases with the length of the free-flowing habitat. As the upstream distance increases, both the distance that must be traveled to reach the reservoir and the opportunities for settling out of the water column also increase. Two parameters, L_0 and L_1, are the free-flowing river lengths associated with a minimum (0) and maximum (P_{sweep}) probability of reaching the reservoir, respectively (Table 1).

Juvenile and adult survival

The PVA model simulates several potential sources of mortality for juveniles and adults, only two of which apply in these simulations. First, white sturgeon ages 1 and older are exposed to a baseline mortality of S_j for juveniles and S_a for adults (Table 1). Second, individuals that migrate downstream are exposed to entrainment mortality (see Model description in main text).

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Chutes and ladders and other games we play with rivers. II. Simulated effects of translocation on white sturgeon

Henriette I. Jager

Abstract: Restoring connectivity is viewed as an important recovery option for fish species adversely affected by river fragmentation. This simulation study quantified the genetic and demographic effects of translocation on metapopulations of white sturgeon (*Acipenser transmontanus*) inhabiting a series of long (source) and short (sink) river segments. Genetic effects were predictable; upstream translocations increased introgression and downstream translocations had no effect. Demographic results suggest that indiscriminant efforts to reconnect populations may do more harm than good. Simulated river systems with high interspersion of long and short segments and a long segment far upstream tended to benefit most from translocation, but only when narrow screening or downstream passage was also provided below the river segment receiving fish. When combined with narrow screening, upstream translocation to a long segment subsidizing several downstream short segments produced the best results. Downstream passage outperformed narrow screening only when the translocation recipient was a short segment in a river system with low interspersion and no long, upstream river segment. This model-based evaluation of reconnection options has helped to refine ideas about restoring populations in fragmented rivers by predicting which options benefit riverine metapopulations as a whole.

Résumé : Le rétablissement de la connectivité est considérée comme une solution potentielle importante pour la récupération d'espèces de poissons affectées négativement par la fragmentation des rivières. La présente étude de simulation permet de quantifier les effets génétiques et démographiques des transferts de poissons sur les métapopulations d'esturgeon blanc (*Acipenser transmontanus*) qui habitent des segments longs (sources) et courts (pertes) de rivière. Les effets génétiques sont prévisibles: les transferts vers l'amont augmentent l'introgression et les transferts vers l'aval restent sans effet. Les données démographiques indiquent que des efforts sans discernement pour relier les populations peuvent causer plus de tort que de bien. Les systèmes de rivière simulés, avec une forte alternance de segments longs et courts et avec un long segment dans la partie amont tout à fait supérieure, ont tendance à recevoir le plus d'avantages des transferts, mais seulement lorsqu'il se fait un tri serré ou lorsqu'il y a aussi un passage vers le bas de la rivière en aval du segment qui reçoit les poissons. Combiné à un tri serré, un transfert vers l'amont à un segment long de rivière, qui alimente plusieurs segments courts en aval, produit les meilleurs résultats. La présence d'un passage vers l'aval donne de meilleurs résultats que le tri serré seulement lorsque le segment de rivière qui reçoit les transferts est court, qu'il fait partie d'un système hydrographique avec peu d'alternances et qu'il n'y a pas le long segment en amont. Cette évaluation des choix de rétablissement des connexions à l'aide des modèles contribue à préciser les théories sur la restauration des populations dans les rivières fragmentées, en prédisant quels choix sont avantageux aux métapopulations des rivières dans leur ensemble.

[Traduit par la Rédaction]

Introduction

Dams have transfigured the landscape of large rivers in the United States and elsewhere. Fragmentation by dams has caused localized extinctions of fish species and reduced diversity of native, river-adapted fishes upstream of high dams (Peter 1998; Pringle et al. 2000; Gehrke et al. 2002). Migratory fishes experience a particularly high risk of local extirpation after losing access to upstream habitat needed to complete their life cycle (Waidbacher and Haidvogl 1998). These negative consequences are blamed, in part, on the fact that dams isolate populations by preventing upstream movement and restricting downstream movement of fishes.

It is widely believed that river connectivity enhances the viability of fish populations (e.g., Fausch et al. 2002). Connected fish populations share access to more diverse habitat, thereby fulfilling seasonal and life-stage-specific habitat needs (Schlosser 1991). In the shifting, dynamic landscape of rivers, access to refuge habitat, though rarely needed, is likely to be important (Schlosser 1991). This is especially true for long-lived species like sturgeons, which, for example, occasionally require free-flowing habitat as refuge from summer episodes of low dissolved oxygen in some reservoirs (Jager et al. 2001). Connected metapopulations of fishes are more likely to be recolonized by neighboring river seg-

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ments after local extirpation, an event that is more likely in short river segments fragmented by dams. The paradigm described above suggests that reconnection of river segments currently separated by dams should benefit riverine fish populations.

Reconnection can be accomplished by building structures that allow voluntary movement or by assisted fish movement by translocation. Trapping and transporting fish around a dam is less expensive in the short term than constructing passage facilities (Cada and Sale 1993). Translocation has several drawbacks. Maintaining connection via translocation requires a long-term commitment to intervention. Because movement is not voluntary, translocation requires understanding the spatial life history and habitat requirements of the species. For example, it might be counterproductive to move juveniles upstream in a species that, left to its own devices, would choose to move upstream only to spawn. Finally, genetic homogenization becomes a concern when fish are moved between distant populations. For species adapted to local conditions, introgression could potentially reduce fitness.

Fish translocations are typically used to reintroduce a rare species to previously occupied habitat, not to reconnect populations. Fish reintroductions have succeeded in some cases and failed in others. Minkley (1995) estimated that only 30% of reintroductions in the arid southwest succeeded. Translocations that released individuals into good habitat have been more successful. For example, translocations of cutthroat trout (*Oncorhynchus clarkii clarkii*) succeeded only in sufficiently large watersheds having deep pools, but not in higher elevation headwater reaches (Harig and Fausch 2002).

The success of translocation programs designed specifically to establish upstream reconnection has not been assessed. To succeed, these translocation programs must meet not only the requirements of translocation in general, but also new requirements specific to adjacent segments separated by dams. Thus, ensuring that suitable habitat is available in the target reach is a first step, after which the effect of the dam on the peculiar, biased metapopulation dynamics of adjacent river segments must be considered. Translocated individuals do not always fare well; 3 of 17 westslope cutthroat trout moved above a dam in Montana, USA, in the hope of providing them access to upstream spawning tributaries ended up below the dam again before spawning season (Schmetterling 2003). Clearly, attention must be paid to downstream as well as upstream movement.

Although upstream movement is most severely curtailed by dams, downstream movement past dams carries its own risks. Without special provisions, fish have but two options: to become entrained into the hydroelectric project or spill over the dam during high flows. Larger fish that are entrained risk being struck by the turbines or the hydraulic forces that they generate. Safer passage around dams can be facilitated by constructing bypass facilities or trapping fish in a downstream segment and transporting them by barge or truck. Screens and trash racks are used to prevent entrainment of fishes. Screening not only reduces entrainment, it also curtails downstream migration and shifts the size structure of emigrants.

This study uses a model of linked white sturgeon (*Acipenser transmontanus*) populations in rivers to understand when translocation is beneficial as a strategy for reconnecting populations. The companion to this paper examines upstream passage (Jager 2006). The costs and benefits of translocation are evaluated with and without mitigation efforts to restrict downstream migration or make it safer. I evaluate translocation in rivers with different combinations of long (source) and short (sink) river segments to better understand how the success of translocation depends on river configuration and the attributes of the segments involved. In summary, the overarching question addressed by this paper is, "Under what circumstances does translocation benefit white sturgeon metapopulations?" The circumstances considered include (*i*) river configuration, (*ii*) attributes of the river segments involved, and (*iii*) assumptions about downstream migration. Answers to this question will provide guidance to those considering translocation programs to help ensure that reconnection efforts have the intended effect of restoring populations of sturgeons and similar fish species in rivers.

Model description

This study uses a population viability analysis (PVA) model to evaluate the benefits of translocation on white sturgeon metapopulations. The PVA model was designed to simulate the population dynamics and future viability of nine isolated white sturgeon populations in the Middle Snake River, Idaho, USA (hereafter referred to as Snake River). Isolation of populations between dams contributes to the fact that only two of the nine Snake River segments now support healthy populations (Cochnauer 1983; Cochnauer et al. 1985). Consequently, methods for establishing upstream connection are of interest.

The goal of this study is to extend results from the Snake River and to seek a more general understanding that can provide guidance for those working to restore fish populations in other rivers. The source–sink dynamics of white sturgeon metapopulations simulated here are driven by segment length. Compared with longer river segments, short segments provide less spawning habitat for white sturgeon and they are more likely to export larvae downstream. Consequently, short segments are considered demographic sinks for this species. I use a PVA model to examine the influence of translocation within the context of this simplified conceptual framework.

Many aspects of the model have been described previously (Jager et al. 2002, 2003; Jager 2006). Here, I describe aspects of the model specifically related to simulating translocation. Because fish can be moved farther using translocation than upstream passage, genetic influences are a concern. Therefore, introgression is also simulated and reported, as described below.

Simulation of translocation

Translocation programs relocate fish from a donor population in one river segment to a recipient population in another segment. The model simulates the capture of white sturgeon in a donor segment, calculates the probability of survival, and

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simulates release of captured white sturgeon into a recipient river segment. The chance of catching an individual white sturgeon, $P_{cap,i}$, is simulated as a function of its size, the size-selectivity of gear, population density, and the annual effort expended in donor river segment j (E_j = 0.1 angler-days·km^{-1}) (eq. 1).

$$(1) \qquad P_{cap} = E_j F_1(D_j) F_2(L_i)$$

The two vulnerability factors in eq. 1 increase from zero to one. Fishing pressure typically increases with fish population density, D_j, in segment j. The density factor, $F_1(D_j)$, follows a Holling type 3 functional response to population density, where the density at which the inflection point occurs is D_h and the limit on daily catch·person^{-1} is F_{max} = 4 (eq. 2).

$$(2) \qquad F_1(D_j) = \frac{F_{max} D_j^2}{D_h^2 + D_j^2}$$

Larger individuals are more vulnerable to capture by anglers and by gear used for translocation (setlines and 2–23 cm mesh, sinking gillnets). With these gears, capture efficiency of encountered white sturgeon increases from zero to one as sturgeon size, L_i, increases from L_{min} = 43 cm to L_{max} = 90 cm fork length (Lepla and Chandler 1995) (eq. 3).

$$(3) \qquad F_2(L_i) = \frac{L_i - L_{min}}{L_{max} - L_{min}}$$

Indicator function, $I_{ini\,move}$ indicates whether a given individual has been captured and survived hooking mortality, S_{hook} = 0.98 (eq. 4). For a donor population with $N_j(t)$ individuals age 1 and older, eq. 5 counts those that survive and are relocated to the specified recipient river segment in year t.

$$(4) \qquad I_{ini\,move} = \begin{cases} 1, & u_i \le P_{cap,i} \cdot S_{hook}, u_i \in U[0,1] \\ 0, & \text{otherwise} \end{cases}$$

$$(5) \qquad \text{Number translocated from } j = \sum_{i=1}^{N_j(t)} I_{ini\,move}$$

Simulation of population genetics

The PVA model used in these simulations keeps track of each individual's genome. Genetic aspects of the model are further described elsewhere (e.g., Jager 2001; Jager et al. 2003). Genetic effects of reconnection scenarios are quantified by comparing final population-level measures of genetic introgression. For a species with homing ability and a strong stock structure, local adaptation is likely, and the goal would be to avoid reconnection options that reduce population subdivision and increase introgression. Otherwise, these effects are less of a concern.

The PVA model quantifies potential for introgression by simulating private alleles, defined as alleles initially present in one population but not in others. In the simulations described here, I simulated a single locus with four private alleles and four shared alleles initially present in each population.

These alleles are passed to future generations by simulating inheritance. After simulating egg production by females in the spawning aggregation (see Reproduction section in Appendix A of Jager 2006), the model simulates the inheritance of alleles by offspring. All males in the spawning aggregation are equally likely to fertilize a given egg. Once the male parent is determined, one of two alleles is drawn from each parent at random at each locus. Normally, mutation would be simulated after inheritance, but the mutation rate was set to zero, so that the only source of new alleles in these simulations is immigration.

Introgression is measured by the number of alien alleles present in each population at the end of the simulation, where an allele is considered alien to a population if it was not present at the start of the simulation. Note that downstream migration results in gene flow from upstream to downstream populations, so that the results do not solely reflect the influx of alleles from translocated individuals. Genetic effects are summarized at the metapopulation level by an index of introgression, the average number of alien alleles, N_{all}, in the final metapopulation.

Simulation experiments

Each scenario was simulated for 20 river configurations representing all possible combinations of three short and three long river segments (see River configurations section in Jager 2006). Simulating a variety of different river configurations provides information on the effects of segment length and upstream–downstream position on the benefits of translocation because these two influences are not confounded. Because individual-based population models are stochastic, results are averages from 30 replicate simulations. Each replicate simulation of a metapopulation of white sturgeon in a river configuration is run for 300 years, which corresponds to approximately 16 generations for this species. (Parameters for these simulations are listed in tables 1 and 2 in Jager 2006).

Fish moved upstream as part of a translocation program might later migrate downstream, risking a fatal encounter with turbines. This suggests that reducing mortality during downstream migration could increase the efficacy of translocation. Turbine mortality can be reduced by providing a bypass route downstream that avoids entrainment into the turbines or by screening fish to prevent entrainment. These two options both reduce turbine mortality, but they differ in where the survivors end up. Screening prevents downstream movement for larger size classes of fish, thereby reducing the downstream migration rate and keeping survivors upstream, whereas downstream passage moves survivors downstream.

Six scenarios simulated are as follows: (*i*) baseline: wide screening alone, (*ii*) narrow screening alone, (*iii*) downstream passage alone, (*iv*) translocation with wide screening, (*v*) translocation with narrow screening, and (*vi*) translocation with downstream passage. Below, the three options without translocation are described in one section and the three corresponding options with translocation are described in the following section.

No translocation with three options for downstream movement

The baseline scenario with no translocation and wide screening corresponded roughly to the current situation in

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the Snake River. For each river configuration, I simulated the response of the metapopulation with (*i*) wide screening, (*ii*) narrow screening, and (*iii*) downstream passage. These simulations included no translocation and were applied to each dam, one at a time. Results of these simulations were used to separate the effects of translocation from those of the downstream mitigation option.

Translocation with three options for downstream movement

All translocation scenarios were simulated with the nominal downstream option (wide screening). Narrow screening (e.g., closer spacing of trash bars) below the dam of the recipient segment reduces the number and size of fish entrained. Simulated screening causes intermediate-sized white sturgeon to be retained upstream, except during high-flow events that cause water to spill over the dam. Narrow screening was simulated only below the segment receiving transplants (screening at the other dams was wide).

Translocation simulations were repeated for a third scenario that simulated downstream passage at the dam below the recipient segment. To simulate downstream passage, all sizes of white sturgeon were permitted to migrate downstream (i.e., no screening), and they experienced no risk of mortality.

Metapopulation responses

One demographic and one genetic response variable are reported here. The demographic index of metapopulation status, NT_{500}, is the sum of final population sizes, where the maximum counted in any population is 500. Truncating at 500 individuals prevents the index from being dominated by increases in already large populations and makes the index more sensitive to increases in small populations. The threshold of 500 individuals is a somewhat arbitrary minimum viable population size first proposed by Franklin (1980).

The ratio of NT_{500} for a given translocation scenario to NT_{500} for the corresponding baseline scenario measures the demographic benefit of translocation. Values greater than one indicate that translocation was successful. Genetic introgression among populations in the metapopulation is measured by the total number of alien alleles, N_{all}, at the end of the simulations, averaged over river segments. The ratio between N_{all} under translocation and that in the baseline scenario is also presented.

Statistical analysis

Patterns that one might expect are as follows. (*i*) Upstream translocations will be more successful than downstream translocations because the recipient population becomes an upstream source supporting downstream segments. (*ii*) Benefits of upstream translocations will be higher when short, sink segments are positioned below the recipient segment. (*iii*) Benefits of upstream translocations will also be higher if there is no long, source population upstream of the recipient segment. (*iv*) Using a source population as a donor will be more successful because it would be better able to withstand removals. (*v*) Translocation will be more beneficial if the recipient segment has the habitat needed to support a growing population (i.e., is a demographic source rather than a sink). However, on this last point, one could also argue that fish moved into a source population are wasted because density-dependent factors would diminish returns.

I conducted a multiple linear regression analysis to determine what circumstances, if any, would lead translocation to increase NT_{500}. The response variable was the ratio of NT_{500} in the translocation scenario to NT_{500} in the baseline scenario. Each observation in the analyses represented one translocation scenario (i.e., one of 30 donor and recipient combinations).

The full model included as explanatory variables attributes of the river configuration and of the spatial relationship between donor and recipient segments in a given translocation scenario. The first two predictors are attributes of a river configuration. LongPosition measures the position (1, 2, 3, etc.) of the long segment farthest upstream. Interspersion describes the number of transitions from a short to a long segment or vice versa. The remaining predictors are attributes that describe the translocation and the segments involved. Distance measures the number of segments between the donor and recipient segment, where a negative number indicates upstream relocation. SubsidizedShorts measures the number of short segments below the recipient segment. LongDonor indicates if the donor segment is long, and LongRecipient indicates whether the recipient segment is long. In the special case when a segment is above the first upstream long segment, these variables are set to the largest possible value plus one (= 7). The largest pairwise correlation between predictors is 0.314.

Sensitivity analysis

Because this is a modeling study, there is a legitimate concern that its results depend on model assumptions. For one river configuration, I therefore evaluated sensitivity of translocation results to several factors, including assumptions about how individuals are captured for translocation and the assumed rate of downstream migration. First, I compared the effect of using effort-based versus quota-based capture of fish for translocation. In both cases, a range of values was examined. Next, I simulated one river configuration (15) with a lower (0.02 $year^{-1}$) and a higher rate (0.07 $year^{-1}$) than that in the simulations reported (0.05 $year^{-1}$). In addition, sensitivity results varying density dependence are reported.

Results

Translocation effects within a river configuration

This section evaluates how translocation influences the river segments involved in a particular river configuration. Translocation showed a general pattern within configurations of decreasing the final size of donor populations and increasing the final size of recipient populations. In 76% of cases (20 configurations × 30 translocation scenarios), the size of the recipient population increased. Whether or not the recipient population increased did not depend on whether it was a long or a short segment. In 73% of cases, the size of the donor population decreased. Decreases were more common among long donor segments.

In addition to main effects on the donor and recipient, two kinds of trickle-down effects were evident. First, the average final population size of the segment directly downstream of

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Table 1. Standardized coefficients for models to predict the demographic index of metapopulation status (NT_{500}) using six predictor variables (rows) that describe the river configuration and the river segments involved in translocation.

Predictor variable	T+W	T+N	T+D	(T+D) – (T+N)	T+W:baseline	T+N:N alone	T+D:D alone
LongPosition	–0.254*	–0.369*	–0.451*	0.091*	0.005	–0.254*	–0.139*
Interspersion	0.592*	0.304*	0.267*	–0.178*	–0.126*	0.188*	0.301*
Distance	–0.007	–0.093*	–0.017	0.118*	–0.019	–0.116*	–0.148*
SubsidizedShorts	0.085*	0.435*	0.275*	–0.358*	0.140*	0.271*	0.123*
LongRecipient	–0.095*	0.324*	0.062*	–0.405*	–0.186*	0.230*	0.104*
LongDonor	0.001	0.006	0.123*	0.112*	0.008	0.006	0.132*
RMSE	76.11	132.6	119	122.8	0.024	0.092	0.061
Adjusted R^2	0.513	0.696	0.466	0.461	0.056	0.313	0.196

Note: Translocation scenarios (T+) are shown with the downstream movement option (W, wide screening; N, narrow screening; D, downstream passage). All models are statistically significant ($p \leq 0.0001$) for 593 degrees of freedom. Asterisks indicate coefficients significant at $\alpha = 0.05$. RMSE, root mean squared error.

the recipient segment exceeded that of the same segment in the scenario without translocation in 61% of cases. Second, the population directly downstream of the donor segment was smaller in translocation scenarios than it was in the baseline scenario in 63% of cases.

Translocation effects among river configurations

This section addresses the question, "Under what conditions does reconnecting white sturgeon populations by translocation benefit the metapopulation?" I discuss the influence of mitigating entrainment mortality during downstream movement and patterns associated with attributes of the segments involved in the translocation.

Wide screening

Translocation with wide screening at each dam, including the dam below the recipient segment, did not benefit the metapopulation. The average NT_{500} among baseline simulations without translocation (mean = 2256, standard error (SE) = 25) was almost identical to the average among translocation scenarios (mean = 2253, SE = 25).

Most variation in NT_{500} was explained by differences among river configurations and not by translocation-related attributes. Translocations in river configurations with high interspersion and a long segment far upstream tended to have high NT_{500} values (scenario T+W, where T denotes translocation, and W denotes wide screening; Table 1). This pattern is driven by differences in metapopulation status among river configurations without translocation (as illustrated in fig. 5 of Jager 2006).

In contrast, there were no patterns in NT_{500} when focusing specifically on variation associated with translocation. The regression model fitted to variation in the ratio between NT_{500} for each translocation scenario and NT_{500} for the corresponding baseline scenario had almost no explanatory power (Table 1).

This lack of pattern is evident when examining differences among river configurations and translocation scenarios visually. Average NT_{500} was not higher among upstream translocations (Fig. 1*a*) and did not increase with the distance moved upstream (Fig. 2*a*). The number of short segments downstream of the recipient segment also had little effect on NT_{500} (Fig. 3).

Translocation-related effects on introgression showed clearer patterns among translocation scenarios with wide downstream screening than NT_{500} did. Simulated translocation from a downstream donor to an upstream recipient increased introgression, but no genetic effects were detected in downstream translocations. Introgression increased as the distance upstream between the donor and recipient segments increased (compare with horizontal lines showing results with no translocation in Fig. 4*b*).

Narrow screening

Narrow screening at the dam directly below the translocation recipient population usually increased average NT_{500} and N_{all} compared with the same translocation scenarios with wide screening at all dams. NT_{500} increased in 88% of cases (river configurations and translocation scenarios), with an average increase of 227 (SE = 8.6). Introgression increased in nearly all cases, by an average of 1.15 alleles (SE = 0.03). Translocation usually improved metapopulation status relative to that in the no-translocation baseline scenario when narrow screening was simulated below the recipient segment.

In the case of narrow screening, multiple regression analysis identified more patterns leading to an increase in NT_{500} than it did with wide screening, collectively explaining nearly 70% of variation in NT_{500}. Higher values of NT_{500} occurred in river configurations with high interspersion and a long segment far upstream and also in those with translocations to a long recipient segment supporting multiple downstream short segments (Table 1).

These patterns are visually apparent. NT_{500} for translocation scenarios with narrow screening was higher for upstream than for downstream translocations (Fig. 1*b*), particularly when sturgeon were moved to a long recipient segment (Fig. 2*b*). The effectiveness of upstream translocations from a long donor to a long recipient segment increased strongly with distance upstream (Fig. 2*b*). This might be because translocations farther upstream result in a larger number of intervening short segments subsidized by the upstream recipient population (Fig. 3).

Partitioning the demographic effect between narrow screening and translocation revealed that translocation augmented the demographic benefits of narrow screening in 36% of river configuration – translocation scenario combinations. In the remaining cases, narrow screening was more (or equally) effective alone. A multiple linear regression model showed that translocation provided added benefits in situa-

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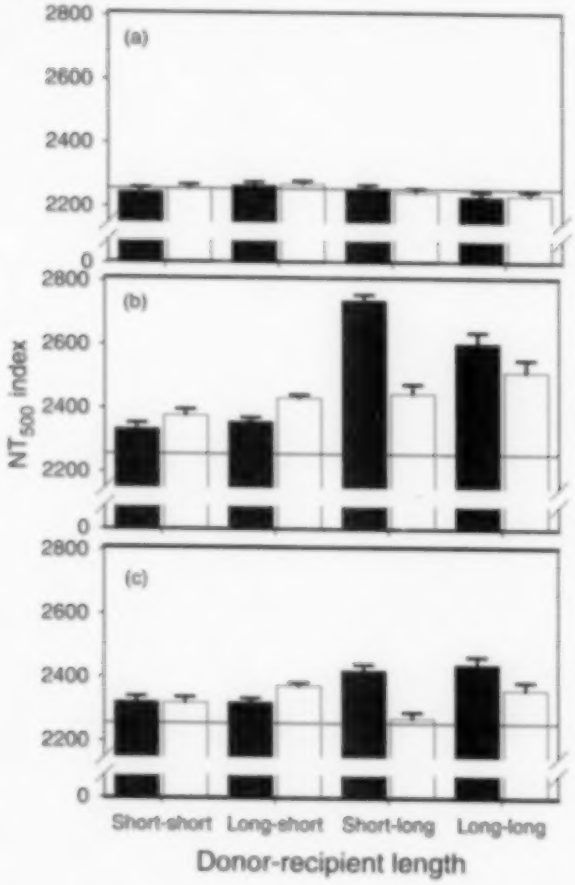
Fig. 1. Comparison of average metapopulation status (NT_{500} + 1 standard error) across river configurations between downstream (open bars) and upstream (solid bars) translocations for each of four combinations of donor and recipient segment lengths (e.g., category short–short on the *x* axis represents the average for translocations from short donor segments to short recipient segments). Three downstream mitigation scenarios shown are translocations with (*a*) wide screening, (*b*) narrow screening, and (*c*) downstream passage. The horizontal reference line shows the average for baseline simulations with wide screening and no translocation.

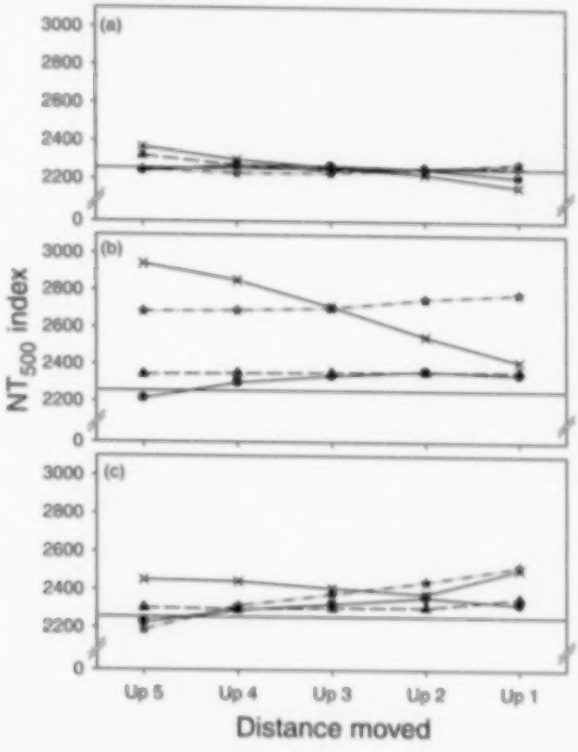


tions when the recipient supported multiple short segments downstream, when a long segment occurred far upstream, when the recipient was a long segment, and when interspersion of long and short river segments was high (ratio T+N:N alone (T, translocation; N, narrow screening) in Table 1). This suggests that one would have to know something about the river and the proposed recipient segment to predict whether the metapopulation would benefit more from the combination than from narrow screening alone.

Downstream passage

For translocation scenarios with downstream passage at the dam directly below the recipient, NT_{500} ranged between 2276 and 2470. Simulations with both downstream passage and translocation generally produced a higher average NT_{500} than the no-translocation baseline scenario (73% of configuration and translocation scenarios) and scenarios with downstream passage alone (59% of cases). NT_{500} was usually higher when compared with the same translocation scenario with wide screening below the dam (87% of cases). Note that connecting two adjacent segments increased NT_{500} compared with the baseline even if they were both short (Fig. 1*c*).

Fig. 2. Longitudinal patterns in average metapopulation status (NT_{500}) for four combinations of donor and recipient segment lengths (circle, short–short; triangle, long–short; star, short–long; ×, long–long). Distance upstream on the *x* axis is measured by the number of segments. Three downstream mitigation scenarios shown are translocations with (*a*) wide screening, (*b*) narrow screening, and (*c*) downstream passage. The horizontal reference line shows the average for baseline simulations with wide spacing and no translocation.



Simulated translocations produced a higher average NT_{500} when the recipient segment was long and upstream (solid bars in Fig. 1*c*). NT_{500} was highest when a long recipient was just upstream of the donor segment. Translocation with downstream passage provided the greatest benefit when sturgeon were moved up from the segment just below the recipient segment (i.e., from below to above the dam with downstream passage), but only if the recipient was long (UP 1 in Fig. 2*c*). This scenario most closely approximated reconnection of adjacent river segments.

A multiple regression model explained 19% of variation in the NT_{500} ratio with both translocation and downstream passage in the numerator and downstream passage alone in the denominator (Table 1, T+D:D alone). Translocation ben-

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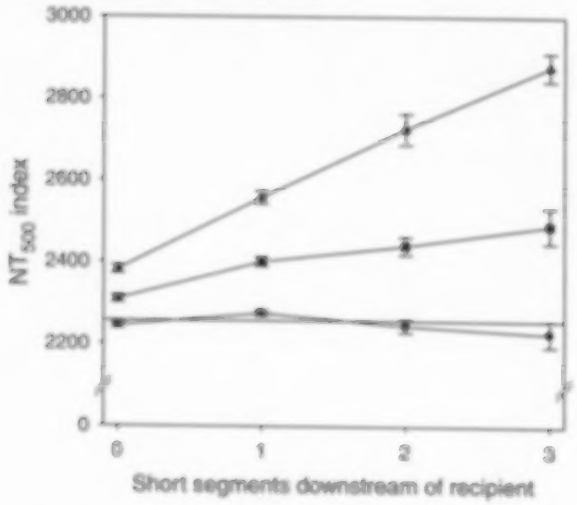
Fig. 3. Patterns in the average metapopulation index (NT_{500}), with bars indicating one standard error, for translocations with zero, one, two, and three short segments downstream of the recipient segments for wide or current screening (circles), narrow screening (triangles), and downstream passage (squares). The horizontal reference line shows the average for simulations without translocation or other mitigation.



efits, over and above those of downstream passage, were greatest in river configurations with high interspersion of long and short segments, in river configurations with a long segment far upstream, and for upstream translocations from a long donor segment.

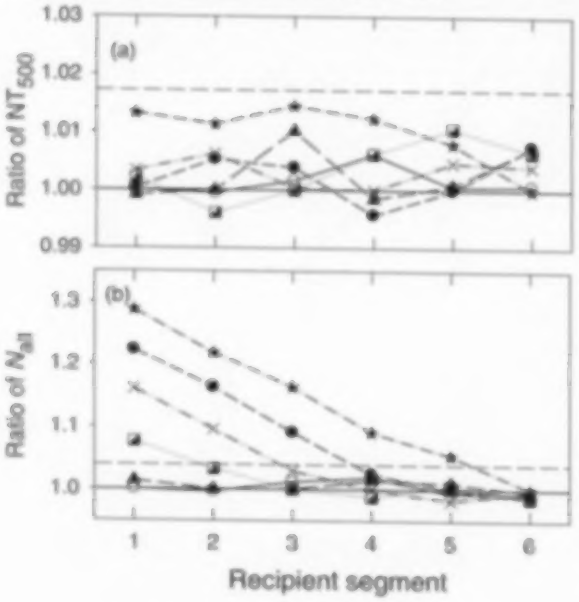
Comparing downstream passage and narrow spacing for each translocation scenario indicated that downstream passage performed better in 21% of cases. A multiple regression analysis of the difference between NT_{500} for the two mitigation options revealed that downstream passage was advantageous in rivers with low interspersion and with short segments upstream (middle column of Table 1). Downstream passage was favored over narrow spacing in translocations from a long segment to a short segment not supporting downstream short segments. Conversely, narrow spacing was favored in translocations of fish far upstream to long segments supporting short downstream segments.

Sensitivity analysis

The simulation experiment to compare effort-based with quota-based translocation shows that effort-based translocation (Fig. 5*b*) is less likely to result in extinction of the donor population (Fig. 5*a*). The decline in average final size of the donor population is steeper under quota-based removal (Fig. 5*a*). The cumulative number of white sturgeon translocated increases linearly under quota-based removal. The cumulative number of fish translocated by effort-based removal reaches an asymptote because it becomes harder to capture sturgeon (i.e., requires more effort) as their numbers decline.

The optimal benefit to the recipient population is reached at an intermediate removal of just under 1500 individuals,

Fig. 4. Metapopulation responses to translocation are measured by ratios of translocation to baseline values for two indices: (*a*) NT_{500}, the index of demographic status and (*b*) N_{all}, the index of introgression. A ratio of one shows no effect on translocation. Different donor segments are shown as different lines and symbols (segment 1, open circle; segment 2, triangle; segment 3, square; segment 4, ×; segment 5, solid circle; segment 6, star). Numbers of segments increase downstream. The broken horizontal line shows one standard error, estimated by 1 + (1 baseline standard error/baseline average index).



regardless of the removal method (Figs. 5*a* and 5*b*). The final size of the recipient population decreases at high effort levels and quotas because of density-dependent factors that are simulated.

Simulations of translocations in configuration 15 with higher and lower downstream migration rates showed the same pattern observed with the nominal value; upstream translocations tended to be more successful than downstream translocations.

In an unpublished case study of the Snake River, I examined the role of density dependence on translocation benefits. The benefits of reconnection generally decreased as density dependence increased in the recipient segment. Simulations reported here imposed density-dependent mortality during the first year, but none thereafter. However, the spawning interval did increase with density. Simulation of density-independent downstream movement, rather than density-dependent movement, had little effect on results.

Discussion

Connecting populations has potential risks as well as benefits. This simulation study suggests that at the metapopulation level, indiscriminate efforts to reconnect populations via translocation might decrease rather than increase metapopulation status in a fragmented river. One con-

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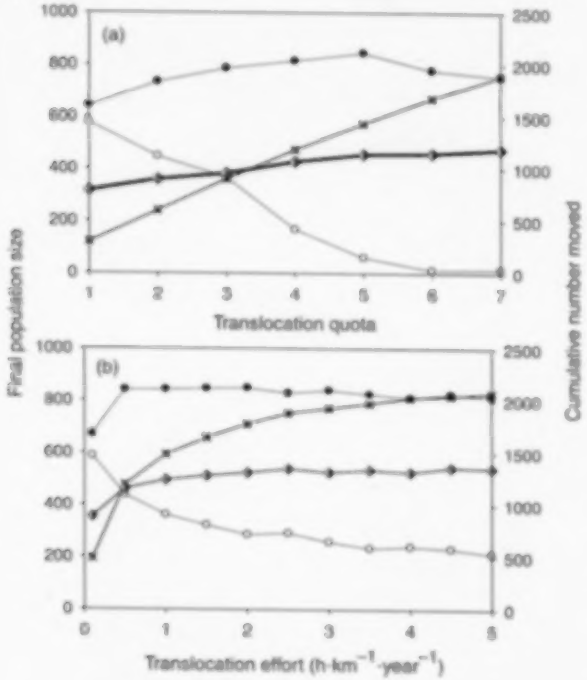
Fig. 5. Comparison of (*a*) quota-based and (*b*) effort-based translocation effects on a long donor (segment 5) and long recipient (segment 1) in river configuration 15. The left axis measures average final population sizes of the donor (open circles) and recipient (solid circles) segment. The right axis measures the total number of fish moved (×) and total emigration from the recipient reach (diamond symbols; to get emigration, multiply axis value by 10).



cern confirmed by this modeling study is that donor populations tend to decrease in size, along with their downstream neighbors. Parameter explorations show this result to be insensitive to the number of individuals moved.

A second concern is that reconnecting populations that are now isolated could have adverse genetic consequences. In this study, simulated translocation from a downstream donor to an upstream recipient increased genetic introgression. Although fitness effects were not simulated here, introgression caused by translocation from populations adapted to conditions in a different part of the river could pose a demographic threat by reducing the average fitness within a population that is already small (Riechert 1993). However, theory suggests that locally valuable alleles will be lost only if the fitness difference is smaller than the fraction of immigrants (Slatkin 1987). Questions remain about the extent to which white sturgeon populations are genetically distinct within, and even among, river systems (Anders et al. 2001). Concerns about local adaptation are warranted when a distant population is used as a donor for a population that has been isolated for a long time.

This study identified specific situations in which translocation was predicted to confer a demographic benefit on metapopulations. First, benefits were greater in certain river configurations: those with high interspersion and a long source segment far upstream. However, translocation did not have clear benefits unless accompanied by either narrow screening (to slow emigration) or downstream passage (to allow safe emigration). Translocation provided the most benefit when the population receiving transplanted fish was in a long segment and positioned upstream, where it could provide support to populations in multiple, downstream, short segments.

Second, downstream passage increased the effectiveness of translocation, particularly when individuals were moved from one long segment to the one immediately upstream. Translocation to the next upstream segment combined with downstream passage most closely resembles a true reconnection of adjacent river segments, although the amount of free-flowing river is still reduced. Note that translocations farther upstream were probably less effective here because they required white sturgeon to pass downstream dams lacking passage facilities. Presumably, providing downstream passage at all intervening dams would improve results for translocations farther upstream.

Narrow screening had a strong positive effect on simulated metapopulation status with or without translocation. By slowing the rate of downstream migration by adults, screening builds populations in long upstream segments. Because small fish (larvae and juveniles) are able to pass downstream safely, the bolstered upstream source population is able to support shorter, sink populations downstream.

The benefits of narrow screening simulated here were probably higher than those that would be realized using other fractional reductions. First, according to the model, reducing screen size by half is near optimal for the downstream segment. If spacing is too narrow, no immigrants arrive from upstream, but if it is too wide, losses to the upstream population result in fewer immigrants (Jager 2006). Second, impingement, which was not simulated here, might reduce the benefits of screening. As the spacing on these devices becomes smaller and more effective at preventing entrainment, fish risk being trapped against the screen or trash rack, particularly in fast-flowing water. Impingement is more of a concern for smaller fish species than for sturgeons and other large fishes to which these results apply. Translocation was more likely to provide an added benefit over narrow screening if the river configuration had a long segment above shorter segments to serve as a recipient far upstream.

These results provide some practical guidance for choosing between preventing emigration from a segment targeted for translocation (narrow screening) or making it safe (downstream passage). If the recipient segment is short and segment(s) downstream are long, the model predicts that downstream passage is preferable. Note that translocation is often contemplated for shorter river segments with declining white sturgeon populations. If the recipient is a long segment upstream of short segments, then narrow screening is predicted to be the better option for the metapopulation.

If these results apply to other ecosystems, they would suggest that (*i*) translocations may not be beneficial if the matrix of habitat between patches is too dangerous, and (*ii*) translocations to a patch of potential source habitat lacking immigration would be most beneficial when the patch is

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surrounded by sink habitats and when the emigration is restricted and safe.

Translocation benefits can be compared with those of upstream passage reported in the companion paper (Jager 2006). Translocation provided an average benefit across river configurations in some cases without mitigating risk during downstream movement, whereas upstream passage was never beneficial without mitigating risk. This result was robust to variations in translocation effort, suggesting that it did not depend on the number of fish that moved, which was higher in the passage simulations. Upstream passage is a special case in which the metapopulation benefits only if trickle-down benefits (more downstream migrants) offset reductions in the donor population below the dam.

Because density-dependent factors moderate demographic benefits of reconnection to the recipient segment and reduce the potential for trickle-down benefits, translocation may be less suitable for recipient segments with strong habitat limitation. This is demonstrated by noting that the benefits of translocations between long segments (source populations) increased with upstream distance between the segments for narrow and wide screening.

I am not aware of field studies against which these modeling results could be compared at present, although a translocation study is underway in the Columbia River. Whereas the success of translocation to reintroduce species to previously occupied habitat has been studied, the success of translocation as a means of reestablishing upstream connection has not. Translocation for the purpose of reintroduction has been less successful than expected, with less than even odds of success (Minkley 1995). This mediocre success has been attributed to failures of one-time reintroductions from distant populations for species with strong local adaptations. Success in selected cases has been attributed to careful attention to the habitat requirements of a species (e.g., Harig and Fausch 2002).

Although no recipe for success of translocation for the purpose of upstream reconnection has yet been discovered, this study suggests ingredients for successful reconnection programs designed for large, riverine fishes that can now be tested in the field.

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State-dependent energy allocation in cod (*Gadus morhua*)

Christian Jørgensen and Øyvind Fiksen

Abstract: Growth and maturation are processes that are tuned to the external environment that an individual is likely to experience, where food availability, the mortality regime, and events necessary to complete the life cycle are of special importance. Understanding what influences life history strategies and how changes in life history in turn influence population dynamics and ecological interactions are crucial to our understanding of marine ecology and contemporary anthropogenic induced change. We present a state-dependent model that optimises life-long energy allocation in iteroparous fish. Energy can be allocated to growth or reproduction and depends in the individual's age, body length, and stored energy and the state of the environment. Allocation and the physiological processes of growth, energy storage, and reproduction are modelled mechanistically. The model is parameterised for Atlantic cod (*Gadus morhua*), more specifically the Northeast Arctic cod stock. Growth and maturation predicted by the model fit well with field observations, and based on a further investigation of cod reproduction in the model, we conclude that the model has the ability to recapture complex life history phenomena, e.g., indeterminate growth and skipped spawning, and therefore provides an important tool that can improve our understanding of life history strategies in fish.

Résumé : Les processus de croissance et de maturation sont ajustés à l'environnement externe qu'un individu est susceptible de connaître et, en particulier, à la disponibilité de la nourriture, au régime de mortalité et aux événements nécessaires pour compléter le cycle biologique. La compréhension des facteurs qui influencent les stratégies démographiques et, inversement, la connaissance de l'impact des changements de stratégie démographique sur la dynamique de population et les interactions écologiques sont essentielles pour interpréter l'écologie marine et les changements anthropiques contemporains. Nous présentons un modèle dépendant l'état qui optimise l'allocation de l'énergie tout au long de la vie chez les poissons itéropares. L'énergie peut être allouée à la croissance ou à la reproduction et elle varie en fonction de l'âge, de la longueur du corps et de l'énergie emmagasinée par l'individu, ainsi que de l'état de l'environnement. L'allocation et les processus physiologiques de croissance, de stockage d'énergie et de reproduction sont modélisés de manière mécaniste. Nous avons inséré dans le modèle les paramètres spécifiques à la morue franche (*Gadus morhua*), plus précisément au stock de morues du nord-est de l'Arctique. La croissance et la maturation prédites par le modèle s'ajustent bien aux observations de terrain; une étude plus poussée de la reproduction des morues dans le modèle nous amène à conclure que le modèle a la capacité de représenter des phénomènes complexes du cycle biologique, tels que la croissance indéterminée et les frayes omises et qu'il fournit ainsi un outil important qui peut fournir une meilleure compréhension des stratégies démographiques chez les poissons.

[Traduit par la Rédaction]

Introduction

Energy use may be divided into three broad categories — survival, growth, and reproduction. These interests are often conflicting as they are crucial for fitness in different ways. When is an individual predicted to grow to increase future reproduction, and when to reproduce? A large size often means high reproductive success, but also low probability of survival until reproduction can finally take place. When is growth predicted to be determinate, and when indeterminate? When is survival probability predicted to influence the optimal adult size? And in the balance between foraging rate and predation risk, when is an individual predicted to hide, and when to feed (Krebs and Davies 1993)?

Energy is limited for an individual, and these questions represent multiple trade-offs in several dimensions that may be at work simultaneously. Energy allocation, how available energy is diverted towards alternative uses, is the mechanism that integrates the trade-offs through shaping the individual's growth trajectory. This trade-off is the essential core of life history theory (Fisher 1930).

Fisheries management is moving towards an ecosystem approach because ecological complexity confounds single-species management. At the same time, human-induced con-

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temporary evolution is identified as a potential driving force behind observed changes in many marine ecosystems (Stokes and Law 2000; Conover and Munch 2002; Olsen et al. 2004). Because life history theory is an obvious link between ecology and evolution, it provides a tool to predict growth, maturation, and behaviour as ecological forcing changes. Alterations in allocation strategies propagate from individual characteristics via population structure to ecological interactions within and between species. This implies that life history theory should be highly relevant for fisheries science, and understanding the logic of life history theory is an integral part of ecosystem management.

Consider, as an example, stock–recruitment relationships. Allocation to reproduction earlier or later in life is likely to influence the entire demographic structure and population dynamics. Both mature biomass and the stock's overall egg production will be affected through changes in maturity-, size-, and fecundity-at-age. Life history theory is, as such, the mechanistic basis for stock–recruitment relationships and therefore central not only in disentangling stock–recruitment relationships today, but also in making predictions in light of fisheries-induced evolution or climate change.

Intuitively, an old individual should perhaps spend its energy differently from a young one, and being large at a given age harbours different opportunities than being small. Age and body length are likely to influence allocation and should therefore be included as states, i.e., information the individual has about itself that may influence energy allocation (Houston and McNamara 1999; Clark and Mangel 2000). It is common knowledge that an individual's condition plays a central role in both growth and reproduction in various fishes (Kjesbu et al. 1991; Burton et al. 1997; Lambert and Dutil 2000). Most organisms in fluctuating environments rely on stores to balance periods when energy is plentiful with periods of energy shortage. Fish and other animals often use lipid stores, either integrated in the muscle tissue (e.g., clupeids) or in the liver (typical for gadoids). Atlantic cod (*Gadus morhua*) belongs to the latter category, and the lipid-rich liver constitutes up to 9% of the body mass among mature fish (Yaragina and Marshall 2000). There is a close relationship between stored energy in the liver and fecundity, and total liver energy in a cod population has been shown to be a good proxy for total egg production (Marshall et al. 1999). Thus an individual's condition, interpreted as the amount of stored energy, directly affects reproductive success and survival.

Earlier life history models investigating energy allocation in fish have used a fixed rule to describe lifelong allocation patterns: all available energy was allocated to growth up to a variable age at sexual maturation, and a fixed proportion of the energy was diverted to reproduction from then on to maximise reproductive value (Roff 1983; Law and Grey 1989; but see also Strand et al. 2002). These models have provided great insight into life history strategies and the evolutionary dynamics of harvested fish stocks, but time is now ripe to extend the analyses. Here, we investigate state-dependent energy allocation in a physiologically realistic model based on the Atlantic cod. Using four discretised state variables (age, length, stored energy, and food availability), our model allows for approximately 6.4 million independent values to describe a four-dimensional allocation hypersurface. In the strict sense, this is also a fixed rule, but the rule is so complex that it specifies what to do in nearly all situations that an individual can encounter throughout life.

Our aim is to formulate a flexible life history modelling tool. The high resolution enables seasonal patterns, as well as optimal size-, age-, and condition-dependent life history strategies, to emerge and introduces great flexibility with a sound biological basis into models of fish growth. The model makes very few life history assumptions, while letting optimisation tools exhibit the best patterns of growth and reproduction. This would also be the growth trajectories supposedly favoured by natural selection, assuming no constraints. We show that the model fits well with field data and experimental work and that it recaptures much of the ecological dynamics of the Northeast Arctic cod stock. In a companion paper, we apply the same model to analyse skipped spawning behaviour of cod (Jørgensen et al. 2006).

Model description

Purpose

We develop a state-dependent model that mechanistically describes energy allocation to growth and reproduction in fish. Because energy is a restricted resource, the life-long pattern in this allocation embodies many of the trade-offs that shape life history. The focus on energy allocation therefore fulfils the purpose of this model, which is to find the optimal life history under varying external forcing (e.g., fishing mortality, migration, and food availability). Throughout, we model the energy allocation processes as mechanistically correct as feasible, while retaining flexibility in how allocation can change with time and state. In this way we can use dynamic programming algorithms to find the optimal allocation pattern under the constraints given by the realistic and detailed description of physiology and ecology.

Structure

The modelling approach in this paper uses dynamic programming to find optimal allocation strategies (Houston and McNamara 1999; Clark and Mangel 2000). The result is a state-dependent energy allocation rule that is a life history strategy. Thereafter, we run population simulations of many individuals following the life history strategy. During these population simulations, age and size distributions emerge, and we can assess the implications of the life history strategy on growth, maturation, reproduction, etc. The model is parameterised for the Northeast Arctic cod stock, which is a long-lived species with iteroparous reproduction. From their feeding grounds in the Barents Sea, the spawners migrate in spring to the Lofoten area where spawning takes place. The rest of the year is used for growth and to rebuild energy stores. The time resolution of the model is months (discrete steps), and for each month, net energy intake is allocated between growth (to increase body size) and reproduction (building energy stores and later gonads). The optimal allocation is found by dynamic programming and depends on four states: age (in months, thus including season); body length (cm); size of energy stores (relative scale); and current feeding conditions. In the model, we consider only female cod.

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Processes

Energy allocated to growth irreversibly increases body length, while stored energy can be used for spawning (migration and egg production) or for metabolism during times when feeding conditions are poor (Fig. 1). Density dependence is not included in the model.

Concepts

Optimal energy allocation is determined for each state combination, with expected reproductive value as fitness measure. The result is a highly flexible multidimensional hypersurface that defines a life history strategy, described by 6.4 million independent points (each point corresponding to a particular combination of the four states). Because rewarding analyses are virtually impossible on such amounts of data directly, we simulated populations of fish realising such life history allocation strategies to let age-, size-, and condition-dependent patterns emerge at the individual and population level. A series of monthly energy allocations results in, e.g., a time series of growth, an age at sexual maturation, reproductive episodes with specific fecundities, and skipped spawning seasons (analysed separately in Jørgensen et al. (2006)). There is no interaction between individuals in the simulated population, and individuals only have information about the four individual states. Food availability is autocorrelated in time to allow for more extended periods of advantageous or unfavourable environment. In the forward population simulation, this is modelled as a stochastic process. Because optimal strategies may use the predictive power of an autocorrelated environment to fine tune allocation strategies (e.g., that a favourable environment is likely to persist for some time), current food availability was included as an extra state.

Initialisation

Juvenile fish were introduced in the model at the age of 2 years and with a body length of 25 cm. Maximum age was set to 25 years, and the model was solved for body lengths up to 250 cm to avoid artificial boundary effects.

Input

Growth and maturation data from the literature were used to test parameter values and general properties.

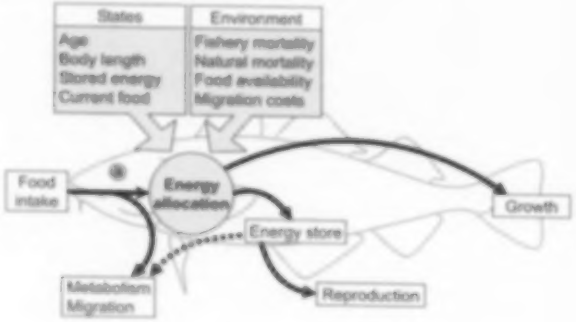
Submodels

Details of the relationships defining the model are given below, followed by specific parameter values chosen to represent the Northeast Arctic cod stock.

Individual physiology

Body mass is divided into two compartments: soma and energy stores. Somatic weight ($W_{soma}(L)$; grams wet weight) includes systematic structures for which growth is irreversible such as skeleton, internal organs, the neural system, and a minimum amount of muscle mass. Additional energy may be stored above this level for reproduction or to enhance survival during periods of food shortage. Because weight usually increases with length with an exponent slightly above 3, the length-specific somatic weight (with no energy stores) can be written as function of $W \propto L^{3+\varepsilon}$, where ε for many species falls between 0.1 and 0.4 (Ware 1978):

Fig. 1. Schematic overview over a life history energy allocation model for the Northeast Arctic cod (*Gadus morhua*). Energy allocation and the states influencing it are shaded. Black arrows indicate energy flow. The dotted arrow indicates that energy stores are drained in periods when food intake cannot sustain metabolic demands.



$$(1) \qquad W_{soma}(L) = \frac{K_{min} \cdot L^{3+\varepsilon}}{100 \cdot L_{std}^{\varepsilon}}$$

where K_{min} is the minimum Fulton's condition factor $K = W \cdot 100 \cdot L^{-3}$, where weight is measured in grams wet weight and length in centimetres (the resulting number varies around 1.0 and describes the fatness or body condition of an individual). For a given length, K_{min} represents the minimum body mass required for structures; death by starvation can be incorporated to occur at K_{min} or with increasing probability as K_{min} is approached. Similarly, there is a limit for how spherical the shape of an individual can be, and K_{max} is the maximum Fulton's condition factor that includes W_{soma} and full energy stores. This maximum reflects the physical limitations imposed by anatomy and the need to maintain other body functions while carrying stores, and in this model, stores cannot be increased above the level set by K_{max}. For $\varepsilon \neq 0$, K_{min} and K_{max} must be specified for a given length L_{std} (cm).

Energy is normally stored partly as proteins by increasing muscle mass and partly as lipids either embedded in the muscles (common for salmonids) or stored separately in the liver (typical for gadoids). The average energy density of these energy stores combined, ρ_E ($J \cdot g^{-1}$), has to be known. We assume that this density is constant, meaning that muscle proteins and lipids are stored at a constant ratio above the minimum muscle mass included in W_{soma}. When the amount of stored energy E (J) is known, total body mass W (g wet weight) can be calculated as

$$(2a) \qquad W(L, E) = W_{soma}(L) + \frac{E}{\rho_E}$$

where E has to be less than or equal to the maximum energy that can be stored, E_{max} (J):

$$(2b) \qquad E_{max}(L) = (K_{max} - K_{min}) \frac{\rho_E \cdot L^{3+\varepsilon}}{100 \cdot L_{std}^{\varepsilon}}$$

Energy expenditure is calculated according to the bioenergetics model by Hewett and Johnson (1992). Metabolic rate (MR; $J \cdot t^{-1}$) is the product of the standard metabolic rate

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(SMR; $J \cdot t^{-1}$) and an activity parameter Act_{std} to include a routine level of activity:

$$(3)\quad MR = SMR \cdot Act_{std} = \kappa_1 \cdot W(L, E)^{\beta_1} Act_{std}, \quad Act_{std} > 1$$

Here, κ_1 ($J \cdot g^{-\beta_1} \cdot t^{-1}$) is the coefficient and β_1 is the mass exponent of the allometric function.

Environment

Food intake ϕ ($J \cdot t^{-1}$) is determined by food availability in the environment and a measure of body size (body mass (W; g) or body length (L; cm)). A stochastic function χ and seasonal cycles $C(t)$ can be incorporated to account for environmental variability in food availability. Feeding intake would thus be

$$(4a)\quad \phi(W) = \chi \cdot C(t) \cdot \kappa_2 \cdot W(L, E)^{\beta_2}$$

or

$$(4b)\quad \phi(L) = \chi \cdot C(t) \cdot \kappa_3 \cdot L^{\beta_3}$$

where $\kappa_2 \cdot W(L, E)^{\beta_2}$ and $\kappa_3 \cdot L^{\beta_3}$ are average food intake for a given body mass or body length, respectively. Typical values for the allometric exponents in fish are $\beta_2 \sim 0.8$ and $\beta_3 \sim 2.5$ (Schmidt-Nielsen 1984).

Energy allocation

For every time step, a proportion $u(a, L, E, \phi)$ of net energy intake will be allocated to storage. The variable u is the core of this model, and when optimised over the entire life span, it represents optimal life history strategies. As such, u balances the trade-off between growth and reproduction and also integrates the effects of natural and fishing mortalities and the environment. Given u, the new state value of the energy stores in the next time step is

$$(5)\quad E(t + 1|u) = E(t) + u(\phi - MR)\delta_{assim}, \quad E \le E_{max}$$

Here, δ_{assim} is the assimilation efficiency for the conversion of ingested energy to stores. The concept of the metabolic rate and the relationship between stored energy and spawned eggs embody energy losses at later steps; therefore this value is commonly higher than the assimilation efficiency for growth of somatic structures (δ_{growth}) below. The proportion $(1 - u)$ is allocated to somatic growth to a new length $L(t + 1|u)$:

$$(6)\quad L(t+1|u) = \left[L(t)^{3+\varepsilon} + \frac{(1-u)(\phi - MR) \cdot \delta_{growth} \cdot 100 \cdot L_{std}^{\varepsilon}}{K_{min} \cdot \rho_S} \right]^{\frac{1}{3+\varepsilon}},$$

$$L(t + 1) - L(t) \le \Delta L_{max}$$

where δ_{growth} is the efficiency with which available energy is assimilated into somatic structures, and ρ_S ($J \cdot g^{-1}$) is the energy density of somatic tissues and is typically lower than the energy density of stores. The equation basically states that growth is allometric with the exponent $(3 + \varepsilon)$, and new tissue is laid down according to available food, assimilation efficiency, and the energy density of somatic tissue. The constraint on maximum theoretical growth rate, ΔL_{max} ($cm \cdot t^{-1}$), acts as an upper physiological limit for length increment per time and can be parameterized from growth studies in food-unlimited immature fish.

Reproduction and migration

Feeding behaviour may be altered during reproduction and possibly also during the migration to and from the spawning grounds. Therefore, the duration of these events must be explicitly incorporated into the time structure of the model. The time required for the migration T_M (t) is the migration distance D_M (m) divided by the swimming speed through the water masses:

$$(7)\quad T_M = \frac{D_M}{(U_S + U_C)}$$

where U_S ($m \cdot t^{-1}$) is the average or typical swimming speed during the migration and U_C ($m \cdot t^{-1}$) is the speed of possible currents that have to be taken into consideration. If $U_C \neq 0$ or the migration route differs to and from the spawning grounds, then T_M and the energetic cost of migration, E_M (J), have to be calculated separately for each direction. For species migrating in groups or schools, U_S will often be identical for smaller and larger individuals.

E_M can then be found from

$$(8)\quad E_M(W, L) = SMR(W)\left[\left(\frac{\kappa_4 \cdot U_S^{1.5}}{L} + 1\right) - Act_{std}\right] T_M,$$

$$E_M \ge 0$$

The expression $\kappa_4 \cdot U_S^{1.5} \cdot L^{-1} + 1$ determines an activity parameter similar to Act_{std} from swimming speed and body size. Other formulations can be used, but a function on this form proved to capture the dynamics of both body length and swimming speed in empirical data for Atlantic cod (Strand et al. 2005) and other fish species (Nottestad et al. 1999).

Stored energy is eventually spawned, and total egg production, b, is proportional to invested energy (Marshall et al. 1999). If migration takes place, energy to fuel migration from spawning grounds back to feeding areas has to be retained, although this constraint may be modified to allow for semelparous life history strategies:

$$(9)\quad b(E) = \kappa_5 (E - E_M)$$

Mortality

A flexible mortality regime incorporating length-, size-, or age-specific natural mortality (M), size- or stage-selective fisheries mortality (F), and additional mortality during migration and spawning (M_S) can be specified. Mortality rates (t^{-1}) are summed, and survival probability S over a discrete time interval T (t) is then given by

$$(10)\quad S = e^{-T(M+F+M_S)}$$

If death by starvation is included, the above equation will apply for $E > 0$, whereas $S = 0$ when $E \le 0$. Details of the mortality regime used for calculations in this paper are given below (Parameters for the Northeast Arctic cod stock section).

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Optimisation algorithm

Optimal life history strategies were optimized using dynamic programming (Houston and McNamara 1999; Clark and Mangel 2000). Models of this type optimise a fitness function by backward iteration through an individual's life history, starting at the maximum age and constantly assuming that the individual acts optimally at every decision point in its future life. A central point is that such models separate between the information available to the individual (here its states), although other factors may affect its success (for instance the development in food availability). Dynamic programming then finds the best response, conditional on the information known by the individual and averaged over possible outcomes. The optimisation problem considered here is thus to find the allocation to reproduction $u(a,L,E,\phi)$ that maximises future expected reproductive value $V(a,L,E,\phi)$ discounted by survival probability S for every combination of the four states (age a, body length L, energy store E, and environment ϕ):

$$(11)\quad V(a,L,E,\phi) = \max_u \left\{ b(E) + S \sum_{\phi(t+1)} P[\phi(t+1)|\phi(t)] \cdot V[a+1, L(t+1|u), E(t+1|u), \phi(t+1)] \right\}$$

Here $P[\phi(t+1)|\phi(t)]$ is the conditional probability of food availability in the next time step given food availability in this time step. To find mean expected fitness, one has to take the sum over all possible states of food availability at time $t+1$. During the spawning season, fitness values for both migrating and nonmigrating individuals were calculated, and the option yielding the highest fitness value was stored.

Parameters for the Northeast Arctic cod stock

The parameters below are selected to describe the physiology and ecology of the Northeast Arctic cod stock (summarised in Table 1). The time resolution is months to allow for seasonal variations in allocation patterns.

Metabolic rate and food intake

The equations for metabolic rate have been parameterised for Atlantic cod by Hansson et al. (1996). At an ambient temperature of 5 °C and with a standard activity level set to $\mathrm{Act}_{std} = 1.25$ (Hansson et al. 1996), monthly metabolic rate MR ($J \cdot month^{-1}$) was

$$(12)\quad \mathrm{MR} = \mathrm{SMR} \cdot \mathrm{Act}_{std} = 2116 \cdot W(t)^{0.828}$$

where SMR is the standard monthly metabolic rate ($J \cdot month^{-1}$).

Food intake at 5 °C was calculated according to Jobling (1988):

$$(13a)\quad \phi(L) = \chi(t) \cdot 276 \cdot L^{2.408}$$

by introducing additional stochasticity of the environment, $\chi(t)$, autocorrelated in time and given by

$$(13b)\quad \chi(t) = \bar{\chi} + C_1 \cdot (\chi(t-1) - \bar{\chi}) + C_2 \cdot N \cdot \sqrt{1 - C_1^2}$$

where N is a random number drawn from a standard normal distribution $N(0,1)$, $C_1 = 0.9$ is the autocorrelation coefficient, $C_2 = 0.15$ scales the variance, and $\bar{\chi} = 0.75$ is the mean of the stochastic distribution. The feeding eq. 13*a* was obtained in farmed cod fed to satiation (Jobling 1988), and $\chi = 1$ would correspond to the same feeding level in the model; by setting $\bar{\chi} = 0.75$, the mean feeding intake in the model is 25% less than for the farmed cod. Cod utilise many different prey species and can switch during unfavourable periods; there is also a maximum feeding rate that sets an upper limit for energy intake; for these reasons, $\chi(t)$ was constrained to fall between 0.3 and 1.5.

Growth

We used $c = 0.065$, which was found from a log–log regression between mean length and weight for Northeast Arctic cod age classes 1–12 measured in the field over the period 1978–2000 (ICES 2003). Maximum and minimum condition factors were set to $K_{min} = 0.75$ and $K_{max} = 1.25$ for a standard length of $L_{std} = 70$ cm (see Appendix A for justification). Maximum length increment was set to $\Delta L_{max} = 18$ cm·year^{-1} and is a constant independent of length in this model, as field and experimental data show that length growth is typically linear with time for food-unlimited immature cod and decreases thereafter as a result of allocation to reproduction (e.g., Jørgensen 1992; Michalsen et al. 1998).

Energy stores

Together, muscle and liver stores vary between K_{min} and K_{max}, and the average energy density of full stores can be calculated provided that we know the energy content and relative contribution of each tissue type. Lipids are stored primarily in the liver, and the liver condition index (LCI) is liver weight expressed as percentage of total body mass. LCI reaches maximum values just prior to spawning; maximum monthly mean values for the Northeast Arctic cod stock are typically 7%–8% in early winter if food is abundant (Yaragina and Marshall 2000). A maximum value that can be obtained by the most successful individuals may exceed the average and was therefore set to $\mathrm{LCI}_{max} = 9\%$. Total liver energy density (LED; $J \cdot g^{-1}$) of full lipid stores in the liver is then given by (Lambert and Dutil 1997; Marshall et al. 1999):

$$(14)\quad \mathrm{LED} = 2.477 \cdot 10^4 (1 - e^{-0.52(\mathrm{LCI}_{max} - 0.48)})$$

The rest of the weight increase due to storage is increased white muscle mass, which has an energy density of 4130 $J \cdot g^{-1}$ (Holdway and Beamish (1984), their table V). The average energy density of full stores can then be calculated to be $\rho_E = 8700$ $J \cdot g^{-1}$. For comparison, whole-body energy density, which includes not only the lipid-rich energy stores, but also all tissue types, peaked at 7000 $J \cdot g^{-1}$ in a study of the chemical composition of cod (Holdway and Beamish 1984). The energy density of somatic tissues was furthermore calculated to be $\rho_S = 4000$ $J \cdot g^{-1}$ from whole-body energy content minus the liver for cod reared at 5 °C in a study on chemical composition analysis of Atlantic cod (Holdway and Beamish (1984), their tables II, III, and VI).

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Table 1. Parameters used for Northeast Arctic cod (*Gadus morhua*) in a model for state-dependent energy allocation.

Parameter	Value and unit	Biological interpretation
ε	0.065	Value of coefficient above 3 for allometric scaling between body mass and length
K_{min}	0.75 g·cm^{-3}	Minimum condition factor at standard length L_{std}
K_{max}	1.25 g·cm^{-3}	Maximum condition factor at standard length L_{std}
L_{std}	70 cm	Length for which K_{min} and K_{max} are defined
ρ_E	8700 J·g^{-1}	Energy density of muscle and liver energy stores
ρ_S	4000 J·g^{-1}	Energy density of somatic tissue
Act_{std}	1.25	Proportional increase in metabolic rate as a result of activity
κ_1	1693 J·g$^{-\beta_1}$·month^{-1}	Coefficient of allometric metabolic function
β_1	0.828	Exponent of allometric metabolic function
κ_2	276 J·cm$^{-\beta_2}$·month^{-1}	Coefficient of allometric feeding function (of length)
β_2	2.408	Exponent of allometric feeding function (of length)
$\bar{\chi}$	0.75	Mean food intake relative to feeding function
C_1	0.9	Autocorrelation coefficient for environmental stochasticity
C_2	0.15	Scaling of environmental stochasticity
ΔL_{max}	18 cm·year^{-1}	Maximum growth rate
D_M	7.8·10^5 m	Distance for spawning migration
U_S	0.3 m·s^{-1}	Swimming speed during spawning migration
U_C	0.1 m·s^{-1}	Speed of northwards current during spawning migration
κ_4	320 cm·s$^{1.5}$·m$^{-1.5}$	Coefficient for empirical cost of swimming function
P_{lipids}	0.63	Proportion of total energy stored as lipids in liver
LCI_{max}	9%	Maximum weight of liver relative to body weight
δ_{store}	0.4	Efficiency of storing ingested energy
δ_{growth}	0.08	Efficiency of building somatic body mass from ingested energy
κ_5	0.256 eggs·J^{-1}	Conversion between stored energy and spawned eggs
M	0.25 year^{-1}	Natural mortality
M_S	0.1 year^{-1}	Increased mortality during spawning and migration
F_F	0.20 year^{-1}	Feeder fisheries mortality
F_S	0.22 year^{-1}	Spawner fisheries mortality
a_{max}	25 years	Maximum age
a_{min}	2 years	Age at which recruits are introduced in the model
l_{min}	25 cm	Length of recruits

It is difficult to estimate energy loss in metabolic reactions, especially when the ingested molecules are only moderately rearranged before, e.g., becoming part of the animal's stores. In general, half the energy in food can be made available as ATP (adenosine triphosphate), and maximum muscle efficiency (energy in ATP versus physical work done) is around 0.45 (Alexander 2003), but we have not been able to find more exact determinations of overall metabolic pathways of relevance to this model. We set the proportion of ingested energy that was preserved when stored to $\delta_{store} = 0.4$. This value is relatively high because lipid and protein storage requires few biochemical rearrangements compared with somatic growth processes, and δ_{store} accounts only for energy lost from ingestion to storage; energy losses during metabolism and production of eggs are taken into account in the empirical relationships in eqs. 9 and 12. Assuming further that the efficiency in converting energy from stores to eggs is also 0.4 and that growing somatic structures such as bones and neural tissue is only half as efficient as the entire process from ingestion to egg production, we ended up with $\delta_{growth} = 0.08$ of the energy being preserved when used for somatic growth. These parameters were chosen also based on predicted growth patterns in terms of length and weight in the model.

Migration and spawning

Each January, fish can either start migration in order to spawn, which occupies January through May, or stay at the feeding grounds. Atlantic cod eat little or nothing during the spawning season (Fordham and Trippel 1999). This has been simplified, and in the model, there is no net gain in energy for fish during migration and spawning ($\phi(W)$ is set to equal $SMR \cdot Act_{std}$). For calculations of energy consumption during spawning migrations, we used $\kappa_4 = 320$ cm·s$^{1.5}$·m$^{-1.5}$ (Strand et al. 2005), $U_S = 0.3$ m·s^{-1} (Brander 1994), and $U_C = 0.1$ m·s^{-1} (Brander 1994). Because the current flows north along the Norwegian coast, $(U_S + U_C)$ was used for estimating required time for the southward migration, whereas $(U_S - U_C)$ was used for the migration north. The migration distance $D_M = 7.8 \cdot 10^5$ m was measured on a nautical map. The required energy for migration was subtracted from the balance in 1 month, although the migration may take longer.

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Stored energy was, for simplicity, spawned in one batch in March. Although there are indications that cod may adjust their spawning intensity between years to compensate for previous reproductive investments (Kjesbu et al. 1996), all stored energy except that required for the northbound migration was used for egg production in this model. Introducing a variable spawning intensity would mean including one more trait in the model; deemed too complicated at present, it suggests a potential direction in the future. In eq. 9, κ_S was set to $0.407 \cdot P_{\text{lipids}}$ (Marshall et al. 1999), where $P_{\text{lipids}} = 0.63$ is the proportion of total energy stored that is stored as lipids in the liver and can be derived from the considerations on energy densities in different tissues above.

Mortality

Growth and maturation in the model are very sensitive to the choice of mortality regime. The mortalities in the spawner and feeder fisheries were chosen to lie between the historic situation (before the onset of trawling) and the current harvesting regime. In evolutionary terms, this would imply that the resulting life history is partly adapted to the new, higher fisheries mortalities (either through contemporary evolution or through phenotypic plasticity that has evolved in response to variable mortality patterns in the past). The simulations in this paper used the following mortalities (all rates per year): natural mortality $M = 0.25$, increased mortality during the spawning (migration) period $M_S = 0.1$, spawner fisheries mortality $F_S = 0.22$, and feeder fisheries mortality $F_F = 0.20$. The spawning season lasts 5 months in this model, so annual mortality rates affecting only spawning individuals was spread evenly over these 5 months. The probability of surviving the next month was thus $S = e^{-(M/12+(M_S+F_S)/5)}$ when at the spawning grounds and $S = e^{-(M+F_F)/12}$ when in the Barents Sea (from eq. 10). The sensitivity to and effects of different mortality regimes are analysed together with skipped spawning in a companion paper (Jørgensen et al. 2006). We have not specified any size-dependent mortality.

Initialisation and constraints

The model starts from age-2 cod, at which individuals were initiated with a length $L_{\text{min}} = 25$ cm (Helle et al. 2002) and 30% energy stores in the forward simulation model. Maximum length had to be defined for the dynamic programming and was set to $L_{\text{max}} = 250$ cm (Brander 1994; Svåsand et al. 1996); this is only a technical limit that has to be well above maximum lengths observed in cod to avoid boundary effects. The model does not incorporate age-specific rates of mortality (i.e., aging) apart from a maximum age of 25 years.

Many of the parameter values above can be used for other cod stocks. Mortalities and details regarding the spawning migration vary between stocks and have to be changed. The physiology remains the same, except for the temperature dependence of food intake (Jobling 1988) and metabolic rate (Hansson et al. 1996).

Results

Comparisons with field data

We illustrate how growth in the model compares with field data from the Barents Sea and the Lofoten area for the period 1978–2000 (Fig. 2; ICES 2003). To obtain the model's prediction of growth, a life history strategy was first found by optimisation using a representative set of parameters including natural and fisheries mortalities. The life history strategy was then simulated in an artificial population where population dynamics, as well as patterns of growth and reproduction, emerge. The desired individual and stock properties were recorded from the simulation, in this case, weight- and length-at-age. For all ages, mean weight- and length-at-age predicted by the model fall within the range of observed mean weight- and length-at-age from field data, and there is no systematic bias.

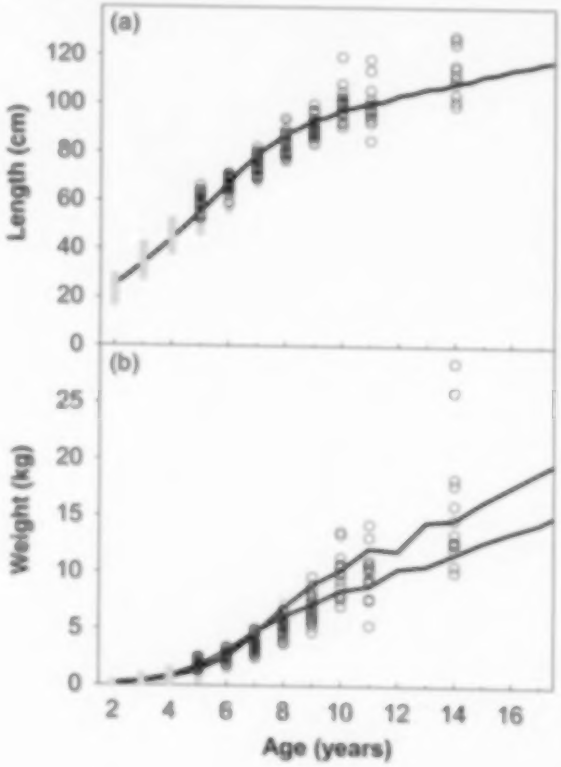

Fig. 2. Predicted length- and weight-at-age from a life history model for the Northeast Arctic cod (*Gadus morhua*) compared with field data. Shaded points are data from the Barents Sea (mostly immature fish), and open circles are from the Lofoten area (mostly mature fish). (*a*) Length (cm) at age (years). (*b*) Weight (kg) at age (years).

The model also predicted the proportion of the stock that would be mature-at-length and -age (Figs. 3*a* and 3*b*, respectively). Mean length at 50% maturation was 78 cm and the corresponding age was 7.5 years. For comparison, field data on the proportion mature-at-age from Lofoten and the Barents Sea combined (ICES (2003), their table 3.5) is also shown (Fig. 3*b*) and does not deviate notably from the model's predictions. The correspondence between the model and field data in terms of growth and reproduction forms the basis for further comparisons between the model and the Northeast Arctic cod stock.

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Fig. 3. Maturity ogives from a life history model for the Northeast Arctic stock of Atlantic cod (*Gadus morhua*). (*a*) Proportion mature as a function of body length (cm). The equation for the logistic regression is $y = 1/[1 + \exp(-0.45(x - 77.6))]$. (*b*) Proportion mature as a function of age in years (solid circles). Shaded squares are field data for the Northeast Arctic cod stock for comparison (from ICES 2003). The equation for the logistic regression is $y = 1/[1 + \exp(-1.7(x - 7.5))]$.

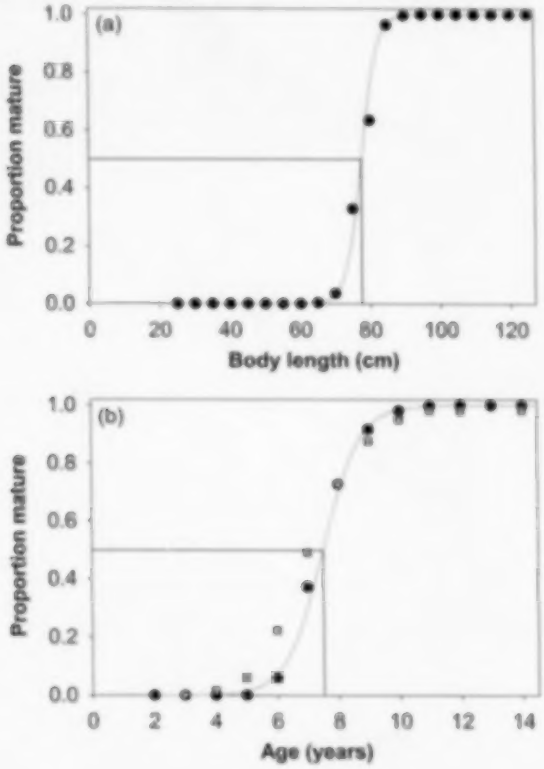
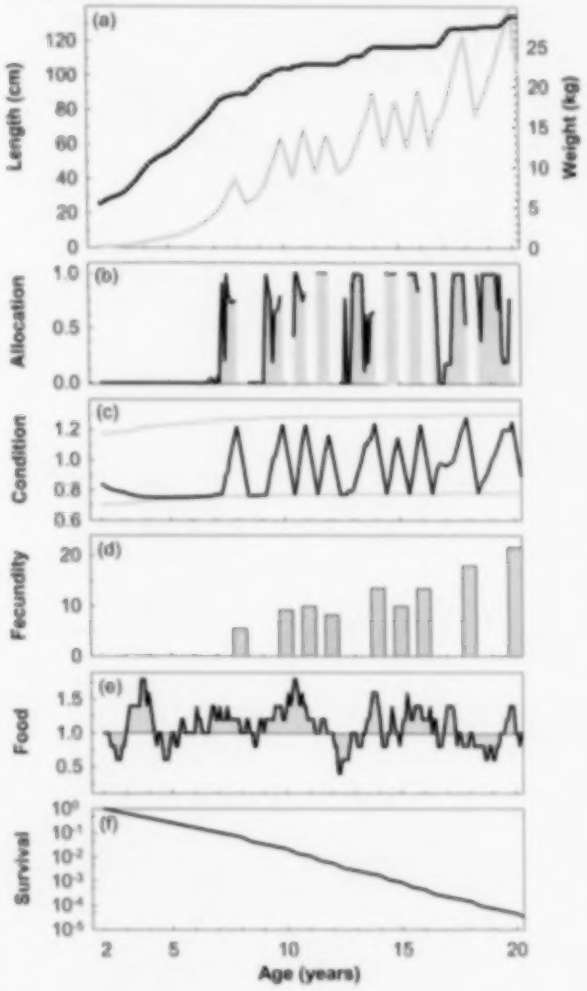


Fig. 4. Growth trajectory and physiology for one individual female cod from a life history model for the Northeast Arctic cod (*Gadus morhua*), simulated in a stochastic environment. The *x* axis shows age and is common for all the graphs. Only one individual's life trajectory is shown in this figure. A population of individuals, each with a corresponding life trajectory, was simulated for the remaining results in this paper. This individual diverted energy towards stores at age 7, approximately 1 year before first spawning to prepare for sexual maturation. (*a*) Length (black line, left axis) and weight (shaded line, right axis). (*b*) Allocation of available energy between energy stores (1) and growth (0). The line shows gaps because no energy is available for allocation during spawning migrations. (*c*) Fulton's condition factor (black line). The shaded lines represent minimum and maximum condition factors attainable at that length; these increase because body mass is proportional to length to the power of 3.065. (*d*) Number of eggs spawned (in millions). (*e*) Food availability in the stochastic environment measured relative to the mean. (*f*) Probability of survival until age (note the logarithmic y axis).



Individual trajectories of growth, allocation, and reproduction

We provide a more detailed picture of how allocation between growth and reproduction shapes the life history of cod by showing growth trajectories in terms of length- and weight-at-age, energy allocation, condition, food availability, survival probability, and the temporal pattern of reproduction for one particular individual cod (Fig. 4). As an immature cod, this individual prioritised growth, and length growth was almost linear with time (Fig. 4*a*). Allocation to stores was low, and only minor energy reserves were kept to balance the risk of starvation (Figs. 4*b*–4*c*). In anticipation of reproduction, allocation shifted from growth to stores at age 7, approximately 1 year prior to the first spawning migration (Fig. 4*b*). The energy stored during this period before reproduction is later used for spawning migration and gonad development. As a consequence of increased allocation to stores, length growth slowed down and the condition factor increased rapidly. Egg production during the spawning season is also shown (Fig. 4*d*). Repeated reproductive events lead to similar patterns throughout the individual's lifetime:

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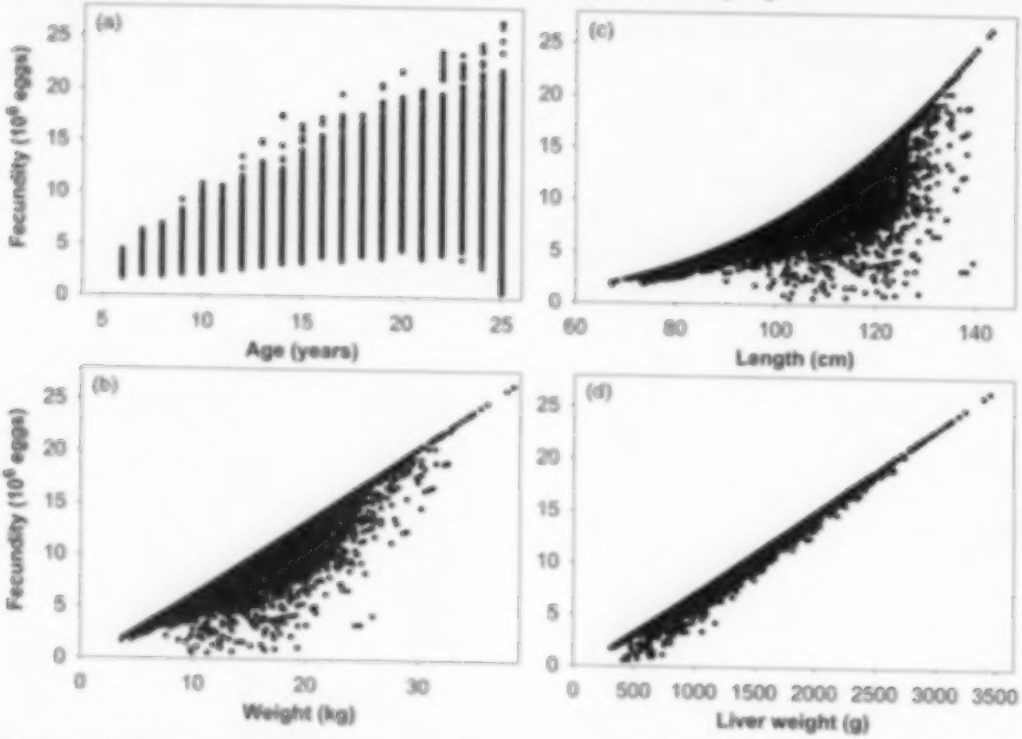
Fig. 5. Fecundity in relation to various individual characteristics. The *y* axis is common for all graphs and shows fecundity in millions of eggs. The results are from population simulation in a stochastic environment for 1000 years. (*a*) Fecundity vs. age (years). (*b*) Fecundity vs. body mass (kg). (*c*) Fecundity vs. body length (cm). (*d*) Fecundity vs. liver weight (g).



allocation to stores prior to reproduction, rapid weight increase and no length growth, followed by reproduction. Curiously, this cod invested all its energy in growth also in some of the years after sexual maturation (e.g., at age 9 and partially at age 13) and skipped spawning entirely in those years. The phenomenon of skipped reproduction is studied more closely in Jørgensen et al. (2006). Food availability (Fig. 4*e*) also influenced growth and reproduction. The variable food availability that this cod experienced while immature lead to concomitant variations in growth rate (visible in Fig. 4*a*). Poor food availability also coincided with skipped spawning at age 13 and age 19. Survival probability until a given age dropped faster when at the spawning grounds as the combined mortality from fishing and reproduction is higher than the fishing mortality at the feeding grounds (Fig. 4*f*; note the logarithmic axis).

Fecundity will vary with the individual's size, its stored energy, and the size-dependent energetic cost of migration. Some relations with fecundity are shown to visualise these effects (Fig. 5). Maximum and average fecundity were increasing with age, but older individuals were also showing a higher variance (Fig. 5*a*). This occurs for two reasons. First, a higher age will reduce the importance of growth per se and will tend to favour reproduction. Because of the terminal age in the model, the expected future lifespan is lower at higher ages. This reduces the value of the future component of reproduction relative to the present, meaning that energy would best be used for reproduction. In economic terms, reproduction is low-risk instantaneous liquidation of available capital (stored energy), whereas growth is an investment in the future, subjected to a payoff that is becoming increasingly more risky with higher age (or, in terms of the strategy, the devaluation rate is increasing with senescence). Second, older individuals are usually larger and will thus spend relatively less energy for the migration. This gives them more leeway than smaller fish, and although small fish were forced to have full energy stores to spawn, spawning fish of larger size would show higher variance in their stored energy.

The relationship between weight and fecundity was also highly variable (Fig. 5*b*), although less so for small fish (up to 7 kg) and for the very few large fish that were realised in the simulated population. The same trend was visible for the relationship between fecundity and length (Fig. 5*c*). It thus seems that age, weight, and length are all poor predictors of fecundity when used alone. Liver weight turned out to be a better predictor of individual fecundity (Fig. 5*d*). The variance around this relationship was highest when liver weight was low, because small individuals with lipid-rich livers and a starved larger individual can have the same liver weight. In the model, liver energy content is the proximate mechanism that determines egg production; the variance around the relationship results because individuals in the population differ in age, size, and stored energy (Figs. 5*a*–5*d*).

Stock and recruitment

The picture looked somewhat different for egg production at the population level (Fig. 6), as variation at the indi-

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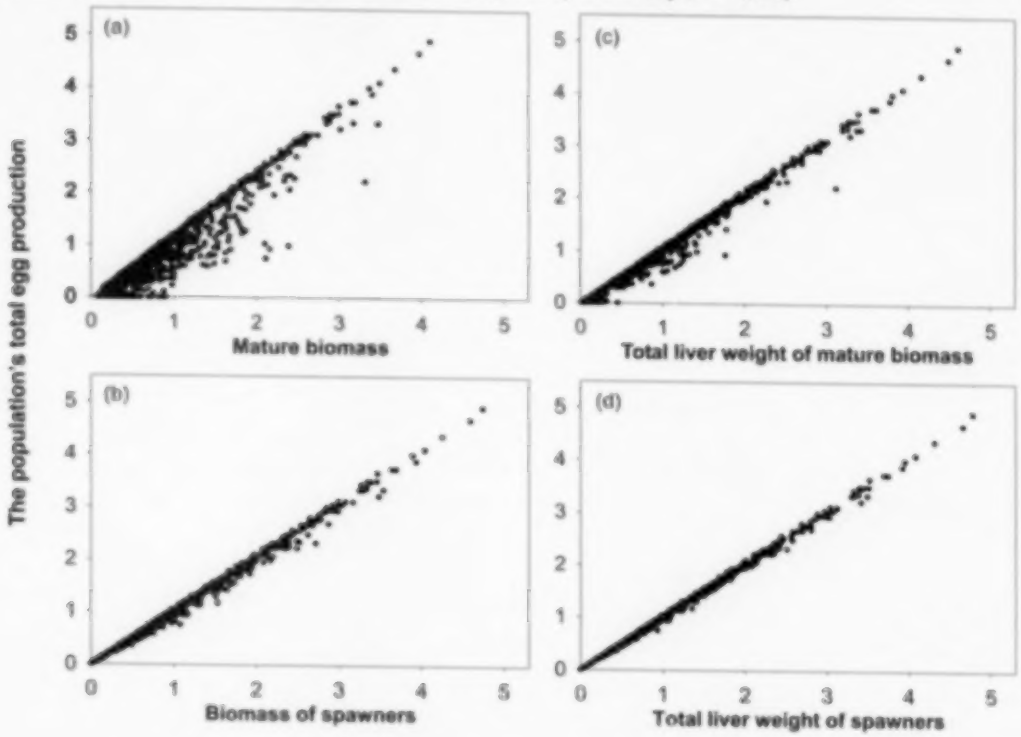
Fig. 6. Comparison of population-level predictors of total egg production in the population. The *y* axis is common for all the plots and shows the total egg production in the population. All axes are normalised to the mean, and the results are from population simulation in a stochastic environment for 1000 years. Coefficients of variation r^2 are given for linear regressions on each data set. (*a*) Biomass of all sexually mature individuals (individuals that do not spawn but that have spawned previously are included) ($r^2 = 0.897$). (*b*) Biomass of spawners only ($r^2 = 0.995$). (*c*) Total liver weight of all sexually mature individuals (individuals that do not spawn but have spawned previously are included) ($r^2 = 0.986$). (*d*) Total liver weight of spawners only ($r^2 = 0.998$).



vidual level may cancel out or become amplified by correlations between individual states in the population. Variance was highest when plotted against total biomass of all sexually mature individuals (coefficient of variation for linear regression $r^2 = 0.897$; Fig. 6*a*). Removing sexually mature individuals that did not engage in spawning removed a lot of the variance (Fig. 6*b*; $r^2 = 0.995$). Liver weight was an even better predictor of egg production at the population level compared with its predictive ability for individual cod (Fig. 6*c*; $r^2 = 0.986$). When the population's total egg production was plotted against total liver weight of only the individuals that were actually spawning, the points fell more or less onto a straight line (Fig. 6*d*; $r^2 = 0.998$).

Maturity and fecundity relationships were also influenced by past food availability (Fig. 7; all values were from January, just before the spawning migration in the simulations). As predictor of mature biomass (defined as all fish that spawned for the first time this year or had spawned previously), the tightest relationship was obtained by averaging food availability over the last two years (Fig. 7*a*). For the stock's total egg production, the best relationship was obtained when mean food availability was averaged over the last year (Fig. 7*b*). The difference in time scales between these two relationships reflect that building gonads is a faster process than increasing mature biomass, which relies on both maturation and growth.

Discussion

We present here a model for energy allocation, parameterised for the Northeast Arctic cod. Because ingested energy can only be used once, the allocation pattern integrates trade-offs between life history components and environmental factors and results in individual growth trajectories and maturation patterns. The model is complex but realistic. It adequately predicts complex life history phenomena such as indeterminate growth, skipped spawning, and variability in age and size at maturation.

We make three assumptions: (*i*) energy can only be used once; (*ii*) energy allocation is optimal at every point in life in the sense that it maximises fitness; and (*iii*) the fitness of an individual is approximated by its expected future reproductive value (true when density dependence acts early in life and the population is in equilibrium (Mylius and Diekmann 1995)). This model makes predictions about life histories from first principles by finding optimal phenotypes. When compared with data, a fit between the predicted life histories and those realised in nature makes it likely that the most important assumptions are built into the optimality

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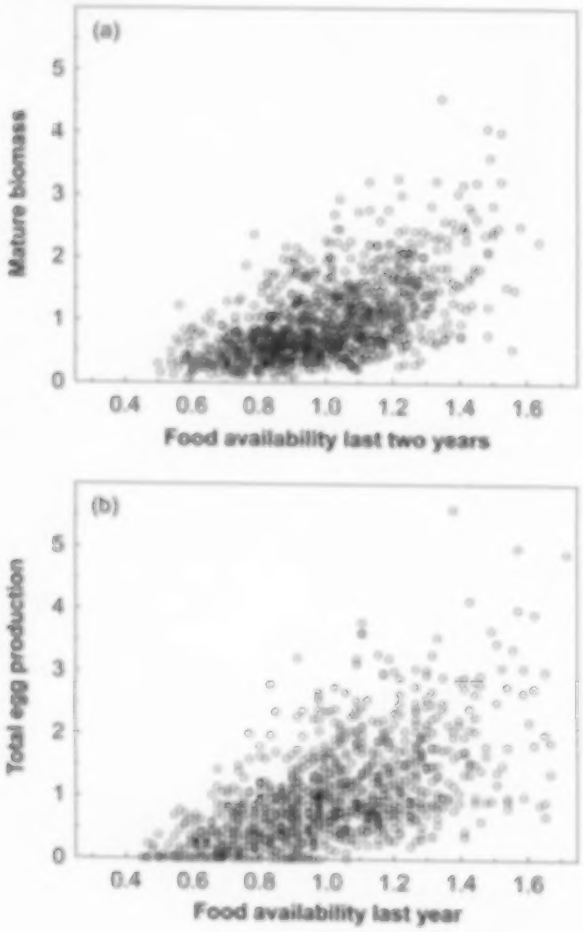
Fig. 7. The influence of mean food availability on population characteristics in January (just before spawning season) in a life history model for the Northeast Arctic cod (*Gadus morhua*). All axes show values relative to the mean. Each point represents one year from 1000 years of simulation of population dynamics. (*a*) In general, mature biomass was higher when mean food availability in last two years was higher. Mature biomass includes effects of increased numbers of fish, increased proportion of mature fish, and increased condition. (*b*) Total egg production for the stock also showed a tendency to increase with increasing food availability.



model and that the model turn can be used to formulate or test hypotheses under a variety of ecological conditions (Sutherland 2005). The model provides a level of detail and realism that can readily be compared with field and experimental data, and the fit in terms of both growth and maturation is promising for further comparisons with field observations.

Abstract versus complex models

Models with many parameters, such as the one presented here, are sometimes accused of being overly complex. Models can be complex in many ways, however. Although our model is rich in mathematical and mechanistic detail, it has a low level of abstraction. Abstract assumptions are replaced by a detailed and realistic formulation of energy allocation. We have aimed at parameters with sound biological meaning and included extensive arguments for the choice of parameter values. Species- and stock-specific parameters are required to make predictions about real-world scenarios. The results presented here are quite robust, as the patterns and results reported in this paper and in Jørgensen et al. (2006) are consistent throughout a wide range of parameter combinations.

Some of the properties of this model that resemble real-world dynamics, such as indeterminate growth, variation in age and size at maturation, and skipped spawning, do not occur if we switch off, for instance, the temporal variability in food intake. In a life history model for the Müller's pearlside (*Maurolicus muelleri*), stochasticity in the environment also lead to bet-hedging strategies and a 2-year life cycle instead of reproduction within 1 year only (Strand et al. 2002). Environmental variability is inherent in biological systems, and the observation that several real-world phenomena only occur when sufficient stochasticity is part of a model suggests that they are adaptations to a variable environment. Furthermore, these adaptations affect population dynamics and ecological interactions. This basic insight is an argument for including stochasticity in models, especially where adaptations are concerned. Much of the rest of the complexity in this model is built around this stochasticity: size has to be included as a state because the variable environment will lead to temporal variations in size-at-age, and storing energy is a means of buffering environmental variation.

Life history optimisation models

This model aptly recaptures complex life history phenomena. Optimisation models have traditionally predicted determinate growth, where allocation should shift abruptly from growth to reproduction at a fixed point in life (e.g., Taborsky et al. 2003). The gradually increasing allocation to reproduction, as seen in the decelerating growth for individuals in our model, is common in nature but only rarely reproducible in models (but see Kozlowski and Teriokhin (1999); indeterminate growth is reviewed by Heino and Kaitala (1996)). Our model also shows that cod may skip reproduction in some years, and this phenomenon of skipped reproduction has, to our knowledge, not previously been reproduced in models (Jørgensen et al. 2006). Growth in the model also fits well with observed growth patterns in terms of both length- and weight-at-age when representative parameter values are used. In summation, we feel confident that the model behaves well and predicts reasonable and realistic growth and maturation patterns, and therefore, the results increase our understanding of the evolution of life history strategies in fish.

In principle, the model (as is typical for dynamic programming models) does not separate between phenotypic plasticity and evolutionary change — it simply finds the optimal life history strategies for a given set of parameters. The reaction norm concept describes the interaction between gene and environment and is relevant for maturation pro-

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cesses as a fixed, genetically determined reaction norm can cause maturation to occur over a range of sizes and ages as the environment changes (Stearns and Koella 1986). The concept has been extended to the probabilistic maturation reaction norm as a method to analyse maturation data (Heino et al. 2002). The rationale behind the reaction norm approach is that size-at-age, which naturally reflects past growth rate, should mean more for the timing of sexual maturation than size or age alone. Because age and length are states, our model includes the phenotypic plasticity described by the maturation reaction norm concept and also uses stored energy as an additional dimension to fine-tune maturation dynamics.

Stock and recruitment

Finding promising proxies for recruitment is essential to successful management of our marine fish stocks. The exercise undertaken in this paper is a good illustration of how different proxies behave in a modelled stock where everything is in principle known. Fecundity is modelled strictly mechanistically and is proportional to the amount of stored energy in the liver (Marshall et al. 1998, 1999). Even though this is a deterministic relationship with no noise added, various measurable individual characteristics perform rather poorly as predictors of fecundity. The best predictor at the individual level, not surprising given the direct link between liver energy stores and fecundity, is liver weight.

The strict upper limit in all the graphs showing fecundity is because of a constraint specified in the model: individual condition factor could not exceed K_{max}. The lower limit of fecundity is more variable and emerges from trade-offs between many factors, e.g., at what combination of age and size should one mature, should one spawn although energy stores are not completely full, would these considerations be modified by the current availability of food, etc. These trade-offs can be solved by the life history approach taken in this paper, and the result is that the lower limit of fecundity or total egg production resembles the variance one can see in real data.

In nature, similar trade-offs determine the maximum fecundity (i.e., the upper limit). For example, how does a bulging belly influence swimming efficiency or feeding (is there room for digestion)? Will large gonads impair the functionality of the swim bladder (Ona 1990)? If so, what are the potential consequences? To what degree will activity level at the spawning grounds influence reproductive success? These trade-offs are harder to model because we know less about them.

By comparing Figs. 5 and 6, it is promising to note that proxies at the population level are better predictors of the stock's total egg production than individual characteristics. In other words, the variable demography of the fish stock removes some of the variation inherent in relationships between individual characteristics and fecundity. A likely explanation for this is that reproduction is normally determined by a few abundant cohorts (e.g., first-, second- and third-time spawners). Over time, the variability of these cohorts between years is less than the total variation between individuals in the population as a whole, and this will tend to reduce the variance when egg production is plotted as a function of population-level characteristics.

At the individual level, liver weight was the best proxy, and this proxy also performed well at the population level. However, excluding the nonspawning part of the population provided even better predictions than using the total liver weight of the mature population. Skipped spawners will contribute to the stock's total liver weight without producing any eggs and will therefore be the source of much of the variation. This goes for both the mature biomass – egg production relationship, as well as the relationship between total liver weight and egg production. The phenomenon of skipped spawning is studied in greater detail in Jørgensen et al. (2006), providing an example application of this model to more complex questions of ecology and life history.

The influence of density dependence

With the optimisation technique used in this paper, dynamic programming, it is not straightforward to find optimal life history strategies when a population is regulated by density dependence (Houston and McNamara 1999; Clark and Mangel 2000). The model can be turned into a dynamic game, but this would require a much more complex model (McNamara et al. 1997). Simulations of population dynamics, however, require that some regulatory mechanism controls population abundance, otherwise the population would go extinct or grow exponentially and infinitely. As a consequence, life history allocation strategies are found by optimisation without density dependence in this model, and the strategy is thereafter simulated in a population where density dependence acts on juvenile survival. The fit between the model's predictions and field data suggests that the model recaptures much of the ecological realism for this stock, even without adaptation to density dependence.

Alternatively, the life history problem outlined in our model could be solved using evolutionary modelling techniques that work also under density dependence. Adaptive dynamics is such a technique (Dieckmann and Law 1996). In practice, making assumptions about how an evolutionary change in one allocation value would incur correlated changes in other values is exceedingly difficult for more than two or a few traits (compared with the 6.4 million values in our model). With this, adaptive dynamics often got stuck in local optima that prevented further evolution (C. Jørgensen, B. Ernande, and U. Dieckmann, personal observation). A second alternative is to simulate evolving populations using genetic algorithms and artificial neural networks to approximate the allocation hypersurface (Huse et al. 1999). These models are, however, hard to trace: it is hard to ascertain when the neural network formulation allows sufficient detail in the allocation hypersurface and whether globally optimal solutions are indeed found or not. We feel that these uncertainties would be harder to accept than any potential effects of density dependence, partly because there is also a weak tradition for including density dependence in models.

In conclusion, there is a promising agreement between field data and the model prediction of growth and maturation. In addition, the model gives a very realistic appearance of reproduction and other ecological interactions. Modelling

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tools such as this one can therefore be used for large-scale experiments that are logistically impossible or awkward in the field or lab. Because the entire population, structured by age, size, and stored energy, is available throughout the stochastic simulation of population dynamics, a large array of various data can be explored in a more experiment-like way (Peck 2004). For instance, the model can be used to study effects of increased fishery mortalities: is the increasing mortality imposed by fisheries sufficient to induce life history evolution (e.g., Law and Grey 1989; Heino 1998; Olsen et al. 2004)? Another example, to which this model has already been applied, is skipped reproduction in fish (Jørgensen et al. 2006). The life history model suggests that the counterintuitive phenomenon of skipped spawning may be more common than previously believed and gives us the opportunity to study the underlying logic. The model provides a tool for large-scale investigations of the life history of cod in different ecological settings. Life history models, such as the one presented here, are powerful tools for investigating driving forces behind instantiated life history strategies, as well as assessing and predicting potential changes derived from altered external forcing such as fisheries and climate change.

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Appendix A. Justification for choice of minimum and maximum condition factors.

Growth in the model was sensitive to the choice of minimum and maximum condition factors. The following reasons for choosing K_{min} and K_{max} were therefore tightly coupled with sensitivity tests and comparisons with growth data. In an experiment following individual cod throughout the spawning season (length 56–87 cm; only females considered here), mean prespawning condition factor was 1.39 (range 1.19–1.75), while the average for spent cod was 0.97 (range 0.81–1.13) (Fordham and Trippel 1999). Using these condition factors for K_{min} and K_{max} in the model, however, gives higher condition factors and weight-at-age than are observed for the Northeast Arctic cod stock. This may be partly because eggs swell prior to spawning by taking up water (Tyler and Sumpter 1996; Fordham and Trippel 1999), which may artificially inflate condition factors for prespawning cod so that they no longer reflect the true size of energy stores. The extent of water uptake can be illustrated by the fact that total volume of eggs spawned was on average 150% of post-spawning body volume in the same study (Fordham and Trippel 1999). Also, cod were fed ad libitum throughout the spawning period in that study, and the easy access to food compared with natural conditions may have improved final condition. A somewhat lower maximum value, $K_{max} = 1.25$, was therefore selected. In a starvation experiment, cod died when condition factors reached 0.44 (range 0.36–0.56; length 31–55 cm), although liver energy stores were depleted before this (Dutil and Lambert 2000). The K_{min} in this model should, however, reflect the condition at which routine energy stores are depleted, not the level to which severe food stress can atrophy muscle mass before death occurs. A value of $K_{min} = 0.75$ was therefore chosen through thorough testing as it reproduced appropriate weight-at-length compared with field data (e.g., Fig. 4). Conditions factors in the model are given relative to a standard length $L_{std} = 70$ cm, which means that realised K_{min} is in the range 0.71–0.74 for the lengths used in Dutil and Lambert (2000).

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The logic of skipped spawning in fish

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Abstract: That sexually mature fish skip reproduction, especially in response to poor condition, has been documented in many species. We present results from an energy-allocation life history model that shed light on the underlying logic of skipped spawning, based on the Northeast Arctic stock of Atlantic cod (*Gadus morhua*). The model predicts that skipped spawning is a regular phenomenon, with up to 30% of the sexually mature biomass skipping spawning. Spawning should be skipped if the expected future gain in reproductive output, discounted by survival, more than balances the expected reproductive success the current year. Skipped spawning was most common (*i*) among potential second-time spawners and (*ii*) early in life, (*iii*) when fishing mortality at the spawning grounds was high, (*iv*) when fishing mortality at the feeding grounds was low, (*v*) when natural mortality was low, and (*vi*) when the energetic and mortality costs associated with migration and spawning were high. Cod skipped spawning more often when food availability was both increased (opportunities for better growth) and decreased (too little energy for gonad development), and this pattern interacted with mortality rate. We conclude that skipped spawning may be more widespread than appreciated and highlight potential consequences for the understanding of stock–recruitment relationships.

Résumé : On a signalé chez plusieurs espèces de poissons que des individus arrivés à la maturité sexuelle omettent de se reproduire, particulièrement en raison d'une mauvaise condition physique. Nous présentons les résultats obtenus par un modèle démographique d'allocation de l'énergie qui illustre la logique sous-jacente à l'omission de la fraye, d'après des données provenant d'un stock de morues franches (*Gadus morhua*) du nord-est de l'Arctique. Le modèle prédit que l'omission de la fraye est un phénomène courant, qui affecte jusqu'à 30 % de la biomasse représentée par les individus sexuellement matures. La fraye doit être omise lorsque le bénéfice prévu du rendement reproductif futur, corrigé pour tenir compte de la survie, dépasse le succès reproductif attendu pendant l'année courante. L'omission de la fraye s'observe le plus communément (*i*) chez les géniteurs potentiels qui se reproduisent pour une seconde fois, (*ii*) tôt dans la vie des poissons, (*iii*) lorsque la mortalité due à pêche sur le site de fraye est élevée, (*iv*) lorsque la mortalité due à pêche sur le site d'alimentation est faible, (*v*) lorsque la mortalité naturelle est faible et (*vi*) lorsque les coûts en énergie et en mortalité associés à la migration et à la fraye sont élevés. Les morues omettent de frayer plus fréquemment à la fois quand la disponibilité de nourriture augmente (une occasion pour une meilleure croissance) ou qu'elle est basse (trop peu d'énergie pour le développement des gonades); ce patron interagit avec le taux de mortalité. En conclusion, l'omission de la fraye peut être plus répandue qu'on ne le croit. Il est possible d'identifier certaines répercutions potentielles du phénomène pour la compréhension des relations stock–recrutement.

[Traduit par la Rédaction]

Introduction

Observations suggest that 5%–30% of mature birds (Cam and Monnat 2000) and as much as 20%–50% of mature fish (Walsh et al. 1986; Schwalme and Chouinard 1999; Rideout et al. 2000) skip reproduction in some populations. These individuals have already undergone the physiological changes associated with maturation and are potentially capable of spawning. Why should long-lived iteroparous individuals skip reproduction after they have reached sexual maturity?

To understand skipped spawning, it is essential to appreciate how the life-long trade-off between reproduction, growth, and survival affects an organism's life history. These trade-offs involve differentially allocating available resources to growth, egg production, and energy storage for future actions. The onset of reproduction has to be timed relative to growth potential and survival probability, and any deviation from the optimal age and size at maturation can lead to great reductions in fitness (Roff 2002).

Skipped reproduction can be analysed on two separate time scales. On the ecological time scale, skipped spawning

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is due to phenotypic plasticity of life history strategies in response to physiological and ecological factors. For instance, it has been documented for several fish species that reproduction is skipped more often when individual condition is poor (e.g., Rijnsdorp 1990; Kjesbu et al. 1991; Rideout et al. 2000). In such cases, the time and energy required for reproduction is better channelled into growth and survival to increase future success rather than exacerbating already low energy reserves by spawning in the current year. Furthermore, this paper presents results that spawning is skipped more often by young or small fish and interprets this in a life history perspective.

Skipped spawning can also be analysed on the evolutionary time scale by assessing how, and to what degree, ecological factors may modify the optimal life history strategy and its consequences on the schedule of reproductive events. Because skipped spawning results from the trade-off between current and future reproductive success, we would expect that factors such as mortality, food intake, and migration costs would influence the optimal life history and thus the frequency and pattern of skipped spawning.

This study explores reproductive strategies in Atlantic cod (*Gadus morhua*) using a flexible life history model. Cod is iteroparous (capable of repeated spawning), and the Northeast Arctic stock, which is the focus of this study, performs annual migrations from the feeding grounds in the Barents Sea to spawning grounds off Lofoten. The annual migrations entail a direct cost in terms of energy and time. Therefore, the potential benefit of reproduction has to be traded off against migration costs, possibilities for growth, and natural and fisheries-induced mortalities. The trade-offs are mediated mechanistically through allocation of ingested energy toward stores or growth; stored energy determines fecundity if reproduction occurs and survival in the event of low prey availability. In the present model, we focus on this allocation rule, which is dependent on age (in months, thus including seasonal variations), body length, state of the energy stores, and food availability. Each point on the resulting hypersurface that describes the allocation rule is independent, so that the allocation rule is not artificially constrained but allows any shape to emerge evolutionarily. The optimal allocation rule, which is also the allocation rule supposedly favoured by natural selection, can then be found for various ecological scenarios. Patterns of growth and reproduction (i.e., life histories) resulting from optimal allocation rules can then be predicted and analysed.

Using the outlined model, this paper first focuses on the physiological and ecological conditions determining skipped spawning on the ecological time scale and then turns to ecological factors that affect the evolution of life history strategies and skipped spawning. Finally, we discuss the results obtained in light of the existing biological knowledge on skipped spawning before highlighting management-oriented issues, namely how exploitation can alter the level of skipped spawning and how skipped spawning may affect stock–recruit relationships.

Model description

Our study is based on a flexible life history model describing a migratory fish (see Jørgensen and Fiksen (2006) for a detailed description of the model). The model is parameterised for the Northeast Arctic cod stock and fits well with observed growth in natural stocks experiencing variable environmental conditions. A key assumption of the model is that energy, ingested in a stochastic feeding environment, may be allocated either to growth or to storage. Growth is irreversible and increases somatic structures together with a minimum amount of muscle mass. Energy stores (lipids in the liver and increased white muscle mass) grow reversibly between a minimum and maximum condition factor, and the stored energy can be utilised for metabolic or reproductive purposes. The model considers only females. Northeast Arctic cod males are generally more active at the spawning grounds and may also suffer a higher mortality when gear that is selective for activity is used. Both effort and success are more related to behaviour for males, which were important reasons to exclude these from the model as data are lacking to parameterise relevant functions.

Eggs are spawned in one batch in March, and reproduction requires migrations to the spawning grounds. Migration is costly in terms of energy (increased metabolic rate during the migration), time (cod eat little during migration and spawning and thus forego opportunities for growth), and mortality (natural mortality increases during migration and spawning). In addition to natural mortality, fishing mortality can occur on the feeding and spawning grounds.

Life history strategies, as determined by the optimal allocation rules between growth and energy stores, were investigated as follows. Firstly, optimal allocation rules between growth and energy stores were calculated using dynamic programming (Houston and McNamara 1999; Clark and Mangel 2000) with four state variables: age (in months, thus including seasonal variations), stored energy (measured on a relative scale between 0 and 1), body length (cm), and food availability. Expected lifetime egg production, discounted by survival probability until spawning, was used as a fitness criterion in the model. Dynamic programming optimizes a life history by maximizing such a fitness criterion backwards through ages, i.e., in our case finding for each age and state combination the allocation rule that maximises the future expected egg production discounted by survival probability starting at the highest age and sequentially progressing towards earlier ages. For each age and state combination, it was also checked whether spawning was preferable or not by calculating fitness for both the spawning and nonspawning option; the cod were then assumed to behave according to the option that maximized fitness. Secondly, the population dynamics of individuals following the previously determined optimal allocation rules were then simulated for 1000 years and subsequently analysed to derive consequences for life history strategies, i.e., patterns of growth, maturation, and reproduction, with a particular focus on skipped spawning. For the purpose of conciseness, life history strategies resulting from optimal allocation rules will be referred to as "optimal life history strategies" throughout the rest of the text.

Investigated fishing mortality scenarios

Three scenarios were used in our investigation of skipped spawning at the ecological time scale, corresponding to different combinations of fisheries mortalities calculated from

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historical and present data for the Northeast Arctic cod stock (O. R. Godø, Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway, unpublished data). Values of annual mortality rates for the spawner fishery (F_S) in the Lofoten area that harvests only spawning individuals and for the Barents Sea feeder fishery (F_F) that harvests all individuals are given.

The first scenario is dominated by a spawner fishery that harvests only the mature part of the population, reflecting the stock's exploitation prior to 1930. The optimal energy allocation rule leads to fish maturing late (at 10.2 years, 117 cm, and 20.8 kg) ($F_S = 0.2$, $F_F = 0.1$). The second scenario mimics the contemporary fishing pressure, where a feeder fishery, harvesting all individuals at the feeding grounds, is the strongest cause of fishing mortality. The corresponding optimal energy allocation rule leads to an early maturing population (at 4.9 years, 51 cm, and 1.6 kg) ($F_S = 0.3$, $F_F = 0.6$). The third scenario uses interpolated fisheries mortalities between the two scenarios (20% of the way from late maturation towards early maturation). The corresponding optimal life history fits very well with growth data for the Northeast Arctic cod stock during the period 1978–2000, with maturation occurring at an intermediate age and size (at 8.1 years, 89 cm, and 8.9 kg) ($F_S = 0.22$, $F_F = 0.20$). The natural mortality was $M = 0.25$ year^{-1} for all scenarios, and there was also an increased mortality during migration and spawning, $M_S = 0.1$ year^{-1}.

Results

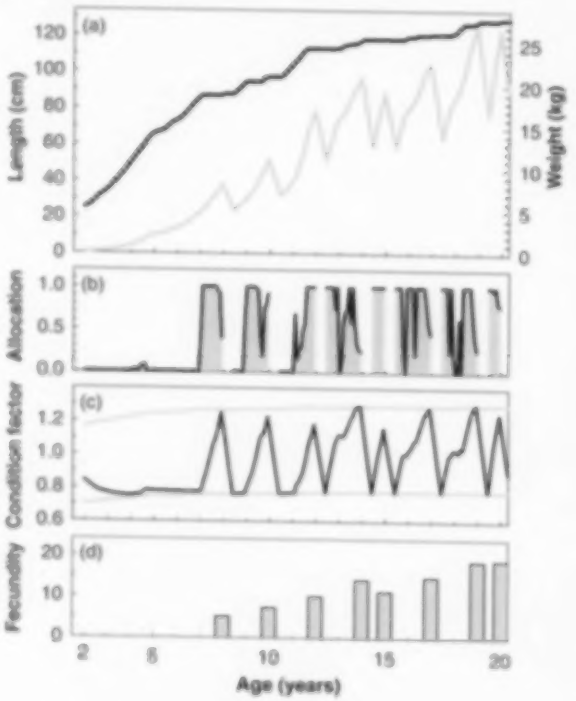
In this section, we first illustrate how energy allocation rules translate into individual life histories. In a second step, we focus on skipped spawning and its pattern with age and other physiological and ecological conditions. This analysis takes place on the ecological time scale, using life histories that are optimal for the three specific fishing mortality scenarios previously defined. In a third step, we zoom out to the evolutionary time scale. By tweaking the ecological parameters of the model one at a time, we present how the resulting optimal life histories and related levels of skipped spawning would change. It appears from these first steps that skipped spawning is a frequent phenomenon over the wide range of parameters tested, with up to 30% of the mature population and up to 60% of potential repeat spawners skipping spawning. In light of these general results, we finally investigate the significance of skipped spawning for effective spawning stock biomass and stock–recruit relationships.

Factors affecting skipped spawning at the ecological time scale

Energy allocation rules and individual life histories

The model has been described in detail by Jørgensen and Fiksen (2006). An example of how allocation of energy between growth and reproduction shapes the life history of one individual cod that skipped spawning several times throughout its life is presented graphically in Fig. 1 (the example is from our third scenario). Briefly, growth in terms of length was nearly linear with time early in life (Fig. 1*a*) when most of the energy was allocated to growth (Fig. 1*b*; values close to 0). Approximately 1 year prior to the first spawning, ingested energy was diverted to stores (values close to 1 in Fig. 1*b*), and this energy was spawned as eggs during the first spawning season (Fig. 1*d*). After first spawning, the individual in this illustration gave priority to growth for another 5–6 months, with little allocation to energy stores, before it once again prepared for spawning. The first and second time this individual spawned (at ages 8 and 10, respectively), it had nearly full energy stores. That fecundity increased by as much as 40% between these two spawning events is due to the strategy of skipping spawning at age 9 and giving priority to a larger body size. On average, fecundity increased 36% every time this fish skipped spawning (at ages 9, 11, 13, 16, and 18).

Fig. 1. Growth trajectory and physiology for one individual female cod from a life history model for the Northeast Arctic cod (*Gadus morhua*), simulated in a stochastic environment. The *x* axis shows age and is common for all the graphs. (*a*) Length (black line, left axis) and weight (shaded line, right axis). (*b*) Allocation of available energy between energy stores (high values) and growth (low values). The line shows gaps because no energy is available for allocation during spawning migrations. (*c*) Fulton's condition factor (black line). The shaded lines represent minimum and maximum condition factors attainable at that length; these increase because body mass is proportional to length to the power of 3.065. (*d*) Number of eggs spawned (in millions). In preparation of sexual maturation, this individual cod directed all its energy was towards stores approximately 1 year before first spawning.



Trends in skipped spawning in relation to age

Spawning was skipped with a stable frequency of around 10% in the early maturing population, and there was no trend with age (Fig. 2*a*). In the other two scenarios, skipped spawning was most common among young fish, before it

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stabilised at 25% and 35% for older fish in the scenarios with intermediate and late maturation, respectively.

The pattern becomes even clearer when the frequency of skipped spawning is plotted against the number of years since maturation (Fig. 2*b*). The stochastic environment led to interannual variation in age at maturation, and this variation was removed by subtracting age at maturation from the age at which spawning was skipped. In all scenarios, the year following maturation showed the highest frequency of skipped spawning, with as much as 90% skipped spawning in the late-maturing population (scenario 1, shaded curve). As the number of years after maturation increased, the frequency of skipped spawning in the early-maturing population (scenario 3) stabilised quickly at the expected level of 10%. For scenarios 1 and 2, the frequency of skipped spawning showed dampened oscillations, i.e., a pattern where spawning was skipped more often every second year, and gradually became more uniform with age. The drop at old ages is a terminal effect of the model, where individuals die at the maximum age of 25 years. It can be interpreted as a very strong senescence effect that reduces the value of future reproductions. A gradually increasing mortality rate at high ages would soften this effect, but the overall picture of higher investment in reproduction towards life's end because of senescence would remain. The curves shown in the figure stop when no more individuals were alive.

Effects of condition and food intake on fecundity and skipped spawning

The optimised life history strategies were flexible enough to respond to variations in food availability. Population fecundity increased when food was abundant; the direct effect on fecundity is mediated through changes in condition factor, where more stored energy allows for more eggs being spawned (Jørgensen and Fiksen 2006). An indirect effect could also be observed: skipped spawning became less frequent as the average condition factor of the mature population increased, thus explaining a substantial part of the population level fecundity increase with food availability (Fig. 3*a*). Smaller cod needed full energy stores to spawn (Fig. 3*b*), whereas larger cod spawned also when less energy was stored. The stratification of points is due to the discretisation of the feeding environment in the model (Fig. 3*b*; points not conforming to this pattern are first-time spawners or correspond to spawning events that take place after spawning has been skipped).

Life history evolution in light of ecological conditions

The following results present optimal life histories (i.e., the life history strategy supposedly favoured by natural selection) under various ecological conditions. For each parameter combination, the optimal life-long pattern of energy allocation was found, and the resulting life history strategies were determined by simulating the corresponding population dynamics. Each point on the surfaces in Figs. 4–6 thus represents the life history that is realised at the predicted evolutionary end point under that specific combination of parameters.

Variation in fishing mortalities

Mortalities that affected only parts of the population had a strong impact on the optimal life history strategy. Mortality on the feeding grounds had a much more pronounced effect than mortality on the spawning grounds (Fig. 4). Characteristically, the two types of mortality also had mostly opposite effects (Figs. 4*b*–4*d*). The proportion of potential repeat spawners that skipped spawning depended primarily on the feeder-fishery mortality (Fig. 4*b*). The seemingly contradictory picture in Fig. 4*a* is the result of demographics, as first-time spawners make up a larger fraction in populations where sexually mature individuals are strongly harvested. As

Fig. 2. The proportion of potential repeat spawners that skip spawning (by biomass) for Northeast Arctic cod (*Gadus morhua*): (*a*) plotted by age (age class), (*b*) plotted against the number of years since maturation. In this representation, the variation stemming from differences in age at maturation is removed. The three curves represent different combinations of spawner (F_S) and feeder (F_F) fishery mortalities giving rise to populations with different maturation strategies: a late-maturing population ($F_S = 0.2$, $F_F = 0.1$; shaded line with solid circles), an early-maturing population ($F_S = 0.3$, $F_F = 0.6$; dotted line with shaded circles), and a population described by a set of parameters providing good fit to growth data for the present Northeast Arctic cod stock, implying intermediate maturation ($F_S = 0.22$, $F_F = 0.20$; black line with open circles). Each population was simulated for 1000 years in a stochastic environment.

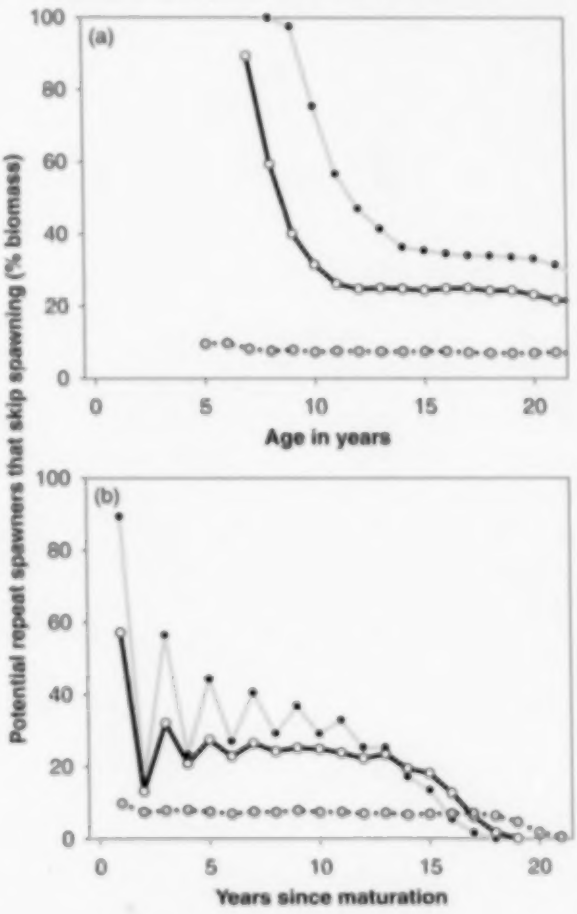

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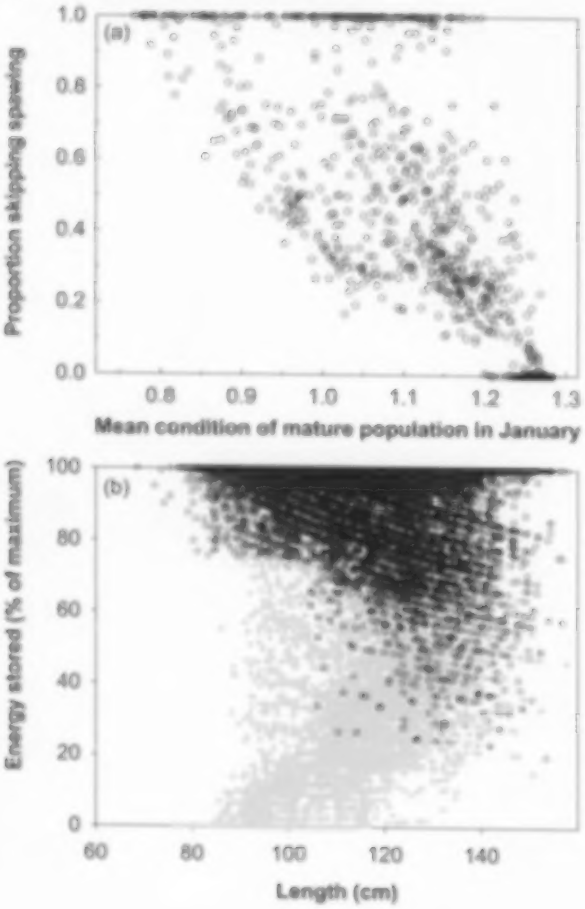
Fig. 3. (*a*) The relationship between average condition in the mature part of the population in January and the frequency of potential repeat spawners that skip spawning. (*b*) The effect of stored energy on skipped spawning. The amount of stored energy, expressed as a fraction of the maximum storage, is plotted against length for all mature individuals. Open black circles denote spawning individuals; solid shaded circles indicate individuals that skipped spawning. The results are from a simulation of population dynamics for 1000 years.



a result, there would be a smaller proportion of repeat spawners and, consequently, also a smaller proportion of mature fish that skipped spawning. Age and length at maturation decreased strongly with increasing feeder-fishery mortality (Figs. 4*c*–4*d*). Under high mortalities on the feeding grounds, the optimal life history implied maturation at 3–5 years of age and at lengths around 30–50 cm. When fishing was confined to the spawning grounds, mean age and size at maturation were 12–15 years and 150–180 cm, respectively.

Variation in mean food availability

Skipped spawning showed a complex relationship when food availability was varied (the left-to-right axis in Fig. 5). This is due to two effects working in opposite directions. When food intake was increased (relative food intake above 1.0 in Figs. 5*a*–5*d*), more energy was available for growth: fish would be larger at the same age and could mature earlier and at a larger size (Figs. 5*c*–5*d*). There would be more years when energy stores could be filled to sustain reproduction, so the increased occurrence of skipped spawning must be due to favourable growth conditions and the advantages that a larger size has on fecundity (Figs. 5*a*–5*b*). This is an effect of the increased value of future reproduction. On the other hand, when food intake was decreased (relative food intake below 1.0 in Figs. 5*a*–5*d*), growth would be slower so that maturation would take place at a smaller size and there would not be food or time to fill energy stores sufficiently in all years. As a consequence, skipped spawning would again increase. Maturation would still take place earlier (Fig. 5*c*), presumably so that individuals could spread the chances of experiencing high enough food availability to sustain migration and spawning over more years. This is probably an effect of the uncertain value of reproduction in any given year.

Variation in natural mortality rate

Varying the natural mortality rate markedly affected both skipped spawning and maturation dynamics (the back-to-front axis in Fig. 5). The general trend was that increasing natural mortality rate favoured early reproduction, resulting in early maturation at correspondingly smaller size, as well as less frequent skipped spawning. The effect of natural mortality is similar but not identical to the effect of the feeder-fisheries mortality; both apply to immature and mature fish at the feeding grounds, but the natural mortality also applies to mature fish at the spawning grounds. Natural mortality is thus not stage selective in the same way as the feeder-fisheries mortality.

The model, as would be expected from the central role of mortality in life history evolution, is sensitive to the exact numerical estimate of this parameter. For the purpose of studying skipped spawning, however, natural mortality changed the overall level but not so much the general or age-related trends.

Variation in migration costs

Not surprisingly, increasing the energetic cost of migration led to a linearly increasing number of skipped spawnings, and the age and length at maturation also increased linearly (Figs. 6*a*–6*d*). This was due to a higher energetic cost for participating in reproduction, favouring a larger size and fuller energy stores. Increasing the level of mortality associated with spawning and migration had similar but less pronounced effects (Figs. 6*a*–6*d*).

Effects of skipped spawning on spawning stock biomass

With earlier maturation, fewer potential repeat spawners would skip, but a larger proportion of the sexually mature biomass would be first-time spawners. The proportion of the sexually mature biomass that was made up of repeat spawners was more or less constant between the three scenarios (Fig. 7).

Discussion

Every year, cod in the Barents Sea are confronted with the choice of whether or not to migrate towards the spawning

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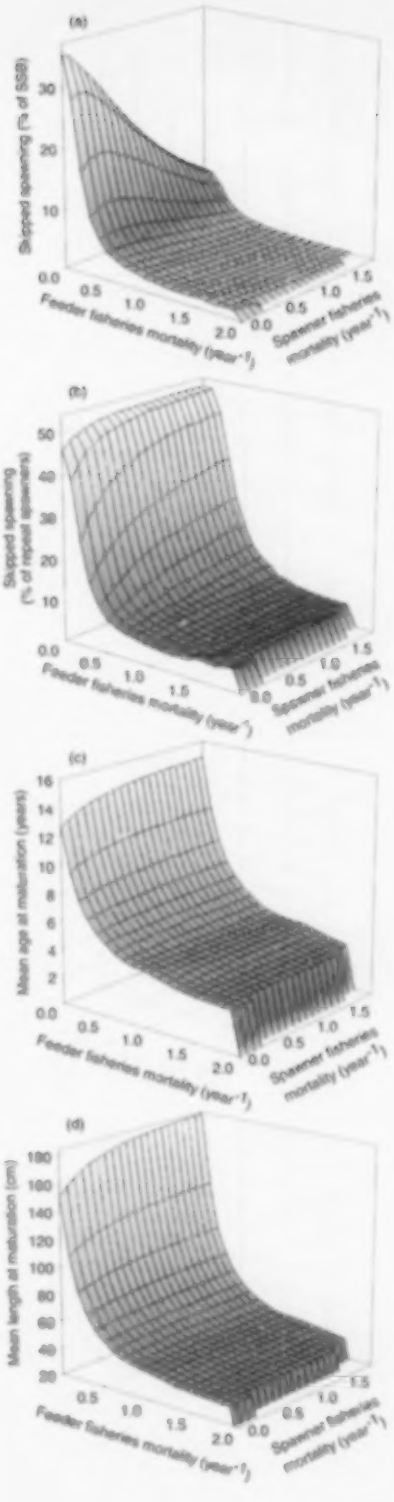

Fig. 4. Effects of varying mortality levels in the spawner and feeder fishery (year^{-1}). At high mortalities in the feeder fishery, the population went extinct; this is visible as the area where the values drop to 0. (*a*) Mean proportion of spawning stock biomass (defined as all sexually mature individuals) that skips spawning. (*b*) The mean proportion of skipped spawning among potential repeat spawners (by biomass). (*c*) Mean age at maturation (years). (*d*) Mean length at maturation (cm). For every grid point, a population was simulated for 1000 years with an energy allocation strategy that was optimised for that specific parameter combination.

grounds. In principle, the decision rule is simple: if an individual skips spawning, the loss in fecundity this year has to be outweighed by the chances of increased egg production in the future, discounted by the survival probability up to that point (Houston and McNamara 1999; Clark and Mangel 2000; Roff 2002). Skipping spawning will thus be beneficial if it sufficiently increases future fecundity or reduces mortality. Our study has shown, however, that applying this rule is not straightforward because of the multiplicity of physiological and ecological factors affecting this balance. To improve our understanding, we will, in the following, provide some background on (*i*) the evidence of skipped spawning in nature and (*ii*) the individual plasticity in female cod reproduction as the physiological basis for skipped spawning. Then, we will examine (*iii*) the causes of skipped spawning in relation to physiological and ecological conditions and (*iv*) how evolution resulting from alterations in ecological conditions may affect skipped spawning. Finally, we will discuss (*v*) how skipped spawning may change on different time scales as a result of human exploitation and (*vi*) how skipped spawning may bias estimates of stock–recruit relationships.

Our model allows for plasticity in energy allocation in response to age, size, energy stores, and food availability and thus for flexible life history strategies. Based on the growth and maturation patterns presented in this paper and in Jørgensen and Fiksen (2006), we conclude that our model's ability to capture complex growth phenomena and trade-offs, together with its flexible response to variations in various conditions within a lifetime, make it suitable for interpreting complex life history phenomena such as skipped spawning.

Evidence of skipped spawning in fish

Bull and Shine (1979) reviewed skipped reproduction among iteroparous animals with a focus on amphibians. Skipped reproduction was most often linked to migration, brooding, or live-bearing and was most common among females. In fish, various studies have identified skipped spawning: Greenland halibut (*Reinhardtius hippoglossoides*; Fedorov 1971; Walsh and Bowering (1981) found reabsorption of oocytes among females attempting to mature for the first time, but no evidence for later skipping), sole (*Solea solea*; Ramsay and Witthames 1996), long rough dab (*Hippoglossoides platessoides*; Bagenal 1957), Norway pout (*Trisopterus esmarkii*; Gokhale 1957), winter flounder (*Pleuronectes americanus*; Burton 1991, 1994), carp (*Cyprinus carpio*; Ivanov 1971), chub (*Leuciscus cephalus*; Fredrich et al. 2003), perch (*Perca fluviatilis*; Holmgren 2003), hake (*Merluccius merluccius*; Hickling 1930), and

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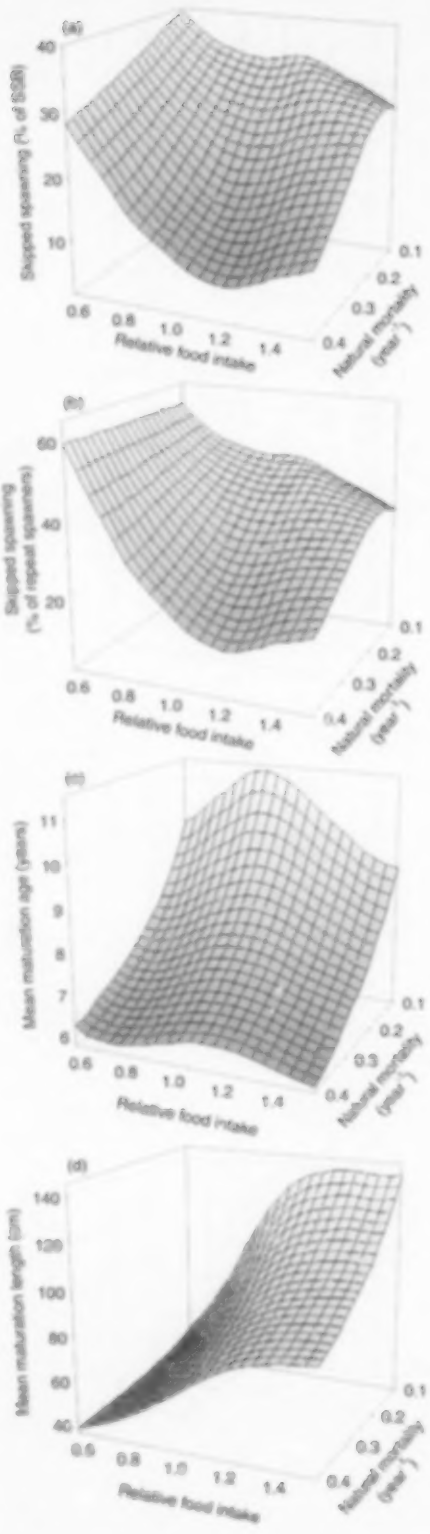

Fig. 5. Effects of varying mean food availability (relative to the intermediate maturation scenario) and natural mortality (year^{-1}). (*a*) Mean proportion of spawning stock biomass (defined as all sexually mature individuals) that skips spawning. (*b*) The mean proportion of skipped spawning among potential repeat spawners (by biomass). (*c*) Mean age at maturation (years). (*d*) Mean length at maturation (cm). For every grid point, a population was simulated for 1000 years with an energy allocation strategy that was optimised for that specific parameter combination.

herring (*Clupea harengus*; Engelhard and Heino 2005). For plaice (*Pleuronectes platessa*), skipped spawning was observed in the laboratory (Rijnsdorp 1990) but not in a long-term data set from the North Sea (Rijnsdorp 1989).

For Atlantic cod, the discussions of skipped spawning began in the 1930s, with the early descriptions portraying a rather contradictory picture. Summarising Russian surveys from the Barents Sea, Messiatzeva (1932) stated that "no more than 10–15% of the fish migrate annually to spawn. The cod does not spawn every year, but apparently only 2 or 3 times in the course of its whole existence". The background data needed to support this statement were not given and have, to our knowledge, not been published. Sivertsen (1935) refuted these claims, suggesting that the problem stemmed from the inclusion of immature age classes, which naturally would explain the low participation in spawning.

References were also made in the older literature to adolescent cod, or "gjelltorsk" (which means sterile cod), large cod with seemingly underdeveloped gonads. Iversen (1934) recorded the gonadal status for cod larger than 70 cm in the Barents Sea. In one location near Bear Island, the proportion of gjelltorsk increased from around 10% in December (prior to the spawning migration) to around 55% in February (when spawning cod should be in Lofoten further south). At some locations, more than 80% of cod larger than 70 cm were recorded as gjelltorsk in February (Iversen 1934, their fig. 8). It seems plausible that at least some of these cod were skipping spawning. At the same time, Rollefsen (1933) argued that these cod were only late-maturing individuals that had not yet reached sexual maturity. Since the 1930s, the issue of skipped reproduction in cod has received little and scattered attention, and it is not a part of managerial considerations today.

In our model, 2%–35% of the mature population skipped spawning. This level of occurrence is consistent with observations published more recently: in Newfoundland, Canada, as much as one-third of cod females were skipping spawning (Rideout et al. 2000), and it was estimated that on average 32% of potential cod spawners on the Flemish Cap skipped spawning in any given year between 1978 and 1985 (Walsh et al. 1986). Growth rates were increasing in the same period (Walsh et al. 1986), meaning that food shortage cannot explain the frequent skipping. Histological examinations of trawl-sampled cod from the Barents Sea just prior to the spawning migration found that up to 57% of potential repeat spawners skipped spawning (Oganesyan 1993). In 1987, during the Barents Sea capelin collapse, no Northeast Arctic cod larger than 90 cm were found on the spawning banks, although they were present in the population (Marshall et al. 1998). In the Gulf of St. Lawrence, Canada, 20%–40% of

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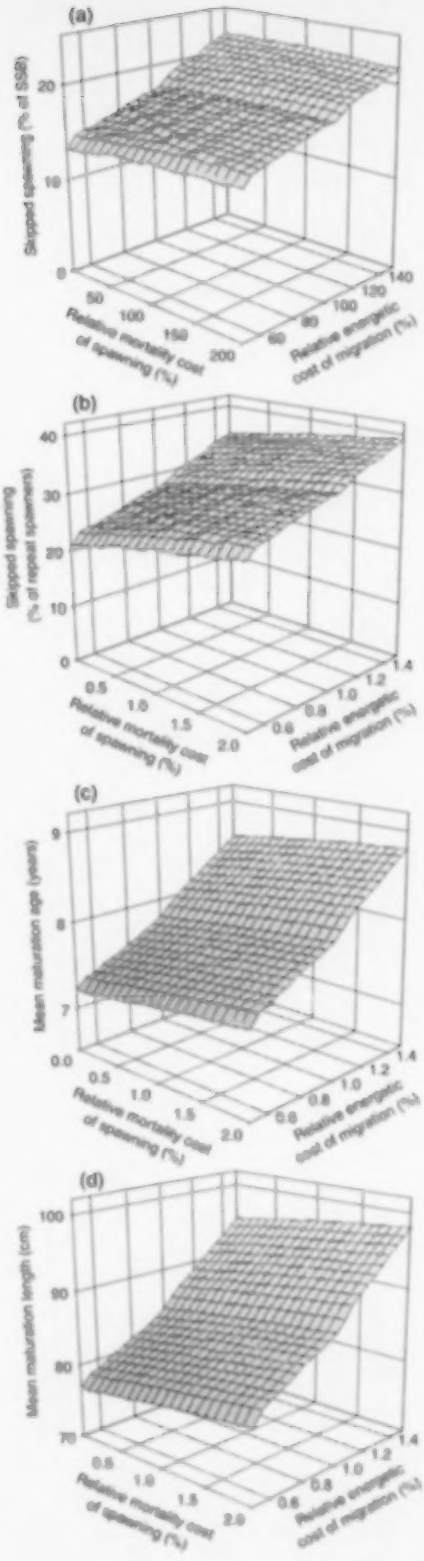

Fig. 6. Effects of the costs of migration in terms of energy and mortality rate on skipped spawning and maturation. The energy required for migration was varied within ±50% of the level used for the intermediate maturation scenario; the additional mortality during the spawning migration was varied within ±100%. (*a*) Mean proportion of spawning stock biomass (defined as all sexually mature individuals) that skips spawning. (*b*) The mean proportion of skipped spawning among potential repeat spawners (by biomass). (*c*) Mean age at maturation (years). (*d*) Mean length at maturation (cm). For every grid point, a population was simulated for 1000 years with an energy allocation strategy that was optimised for that specific parameter combination.

sexually mature cod had underdeveloped gonads at the time of spawning (Schwalme and Chouinard 1999), indicating that they were skipping reproduction this year.

Phenotypic plasticity and the physiology of skipped spawning

Rideout et al. (2005) recently reviewed the physiology and histology of skipped spawning for fish. They argued that methodological problems in identifying the postmature nonreproductive state have lead fisheries science to underestimate its frequency and thus also its importance for recruitment. The timing of sampling is especially important, because signals that may identify skipped spawning are weak or nonexistent during parts of the annual cycle.

Atlantic cod females initiate gonad development up to 7 months prior to spawning (Burton et al. 1997). During that period, impaired or nonimproving feeding conditions may render reproduction less attractive; accordingly, energy temporarily invested in gonads can later be resorbed through atresia (Kjesbu et al. 1991). In laboratory experiments on Atlantic cod, females in poor condition either underwent atresia or skipped gonad development altogether (Kjesbu et al. 1991; Burton et al. 1997). In flatfish, experimental food deprivation induced skipped spawning (Burton and Idler 1987; Rijnsdorp 1990).

From a life history perspective, there is at the same time (*i*) a distinct disadvantage to having a small body size and (*ii*) a clear advantage to being bigger. (*i*) Small fish have higher weight-specific metabolic rates and swim less economically (Schmidt-Nielsen 1984); they thus have a higher energetic threshold for participating in migration and spawning, and a lower share of the energy invested in reproduction is actually used to produce gametes. (*ii*) Fecundity in fish is roughly proportional to body mass, so a 25% increase in length would double fecundity. Add these two effects together and it becomes clear that, for a small migrating fish, growing to a larger size can increase future fecundity to a degree that easily outweighs its current reproductive potential.

It is worth mentioning here that our model does not distinguish between the two physiological mechanisms underlying skipped spawning, that is, atresia and skipped gonad development. In the model, skipped spawning occurs when an individual skips a spawning migration after their first successful reproduction. In reality, this will cover both atresia and cod that skip gonad maturation altogether.

The interpretation of poor individual condition at the beginning of a spawning season is ambiguous, both in the

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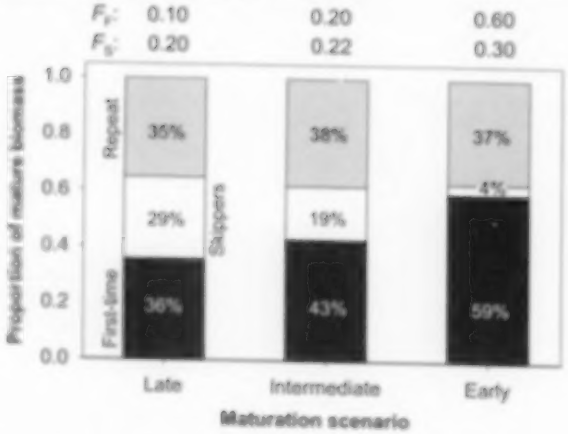
Fig. 7. The proportion of sexually mature biomass that comprises first-time spawners (solid bars) and repeat spawners (shaded bars) and that skips spawning (open bars) for optimal life histories under the three combinations of feeder (F_F) and spawner (F_S) fishery mortalities considered. The values are mean over 1000 years of population simulation.



model and in nature: it can be either a cause for or an effect of skipped spawning. If spawning should be skipped in a certain year for some reason resulting from an individual's life history strategy, then the best option may very well be to give priority to somatic growth and keep energy reserves at a moderate level. This would be recorded as a low condition factor, but the poor condition would be an effect of skipped spawning and thus hard to separate from poor condition stemming from low food availability, which could lead to skipped spawning.

Causes of skipped spawning in relation to physiological and ecological conditions

In the published observations of skipped spawning that linked the phenomenon to ecology or life history, poor feeding conditions were most often identified or suggested as the likely cause (e.g., Burton and Idler 1987; Rijnsdorp 1990; Rideout et al. 2000). On the basis of the potential for phenotypic plasticity highlighted above, we would expect that skipped spawning would be more frequent in our model when an unfavourable feeding environment led to poor individual condition, a concept supported by our model results. Furthermore, we found that it was favourable for larger cod to spawn even when their energy stores were not full, reflecting the benefits that come with a larger body size. The two axes on Fig. 3*b* represent length and energy stores, which were dimensions also in the allocation rule; therefore, the area in Fig. 3*b* where shaded and solid circles overlap indicates when the two additional dimensions, namely current food availability and age, were necessary to fine tune the migration and allocation pattern.

The clear relationship observed between the frequency of skipped spawning and age means that skipped spawning is also an active component in the life history of fish. If low food availability was the only cause leading to skipped spawning, we would expect the frequency of skipped spawning to be relatively stable across all ages, as all age classes suffer from the same environment (we do not consider here the case where subgroups of the mature population utilise different and unlinked food resources; this might apply for Northeast Arctic cod but is not addressed by this study). Poor condition alone probably explains the frequency of skipped spawning in our second scenario (imitating the evolutionary end point of contemporary fishing patterns; the high mortality results in an early maturing population). Spawning was skipped at a frequency of 10% and did not show any variation with age. This life history strategy is geared to value current reproduction much higher than potential future spawnings. Only when individual condition was too low to sustain migration, or when the stored energy could offer only a very limited egg production, was the spawning opportunity totally abandoned.

Skipped spawning occurred more frequently in our first and second scenarios, where mortality rates were lower. A trend with age was also evident: skipped spawning was most common in the years following maturation. Similar results have been found in wild cod, where skipped spawning was most common for cod of small size (Oganesyan 1993). That skipped spawning became less common with age reflects a temporal trade-off in which early growth and later reproduction are favoured. Young cod can spawn potentially many times in the future, and increasing the fecundity for all these reproductive seasons should be attractive. The decision of whether or not to spawn depends only on the comparison of expectations for the current reproductive season with the expected future benefit that comes from a larger size if spawning is skipped. An individual's growth trajectory can thus be roughly divided into three phases: first, only somatic growth takes place up to the age at sexual maturation; second, growth is balanced with reproduction during some years following maturation (mechanistically, growth takes precedence when spawning migrations are skipped more frequently); and third, after that, reproduction receives the full focus of energy allocation and the frequency of skipped spawning stabilises.

The link between skipped spawning and growth has also been demonstrated in perch (Holmgren 2003), to our knowledge, the only work on fish that demonstrates a clear life history trade-off between reproduction and growth after sexual maturation. By back-calculating individual growth from otolith patterns, Holmgren (2003) found that growth was highest in the years when spawning was skipped. This indicates that skipped spawning was not a response to poor food availability, but that spawning could be skipped to redistribute energy towards accelerated growth.

The underlying mechanisms become clearer when the frequency of skipped spawning is considered relative to the age at which maturation takes place. The stochastic environment leads to interannual variations in age and size at maturation, and this variation overshadowed a distinct pattern in how skipped spawning was distributed relative to maturation. In the first 5–10 years after maturation, the frequency of skipped spawning oscillated: a larger proportion of individuals skipped spawning if their age since maturation was an odd number. This corresponds to a life history strategy with a 2-year reproductive cycle during which migration (in order to spawn) and feeding (in order to grow) alternate. With age, these oscillations were dampened. The stochastic environ-

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ment made this age pattern more diffuse with time, which partly explains the dampening. In short, there seems to be two superimposed effects that together can explain the observed age pattern: indeterminate growth causes skipped spawning to be more frequent during the first years after maturation, and a 2-year reproductive cycle creates the oscillating pattern.

Potential evolutionary consequences of altered ecological conditions on skipped spawning

A long and energy-costly migration makes skipped spawning an attractive option, because the saved energy can, if invested in growth, lead to a large increase in future fecundity. As we can observe from the model, the frequency of skipped spawning increases when the energetic costs of migration are higher. The situation is less clear when it comes to the long-term mean food intake, and we can formulate two competing hypotheses. First, we would expect that the potential for a high food intake at the feeding grounds would favour skipped spawning; then the expected gain in future fecundity will rise, making growth an attractive way to spend time and energy. A detail along these lines not included in the model is that cod is normally feasting on migrating capelin on its way toward its spawning areas on the Finnmark coast in northern Norway. This migration overlaps in time with the spawning period of cod, and the concurrent abundance of highly nutritious capelin would thus favour skipped spawning because growth conditions are especially generous this time of year. Second, we might also hypothesise that a lower food intake would result in fewer years with full replenishment of the energy stores, also resulting in more skipped spawning but for other reasons. The results of our model are influenced by both these hypotheses, as can be seen in the increasing occurrence of skipped spawning when food intake was both reduced and increased.

Variations in mortality can affect both phenotypic plasticity (through increasing growth rates in response to relieved density dependence) and evolutionary adaptations (as the balance between current and future reproduction has to be rescaled depending on the expected survival probability). Accordingly, there are ongoing discussions about how best to separate observed life history changes in response to altered fishing pressure into those accounted for by plasticity and those accounted for by genetic change (Heino and Godø 2002; Heino et al. 2002; Olsen et al. 2004). Because there is no density-dependent growth in our model, we discuss the effects of mortality here in this section on evolutionary change.

Increased natural mortality will favour earlier maturation and less skipped spawning, because future reproductive effort will be discounted more heavily. The pattern becomes more complicated, however, when mortalities affect only specific parts of the population, as is the case in the stage-selective fisheries harvesting the Northeast Arctic cod stock (Law and Grey 1989). Low mortality at the feeding grounds compared with the spawning grounds will, for instance, create a mortality refuge for fish that choose to grow rather than spawn and will favour skipping. The model's prediction of late maturation at a large size resulting from this setting corresponds well with observed maturation patterns for the Northeast Arctic cod stock from the beginning of the 20th century (Jørgensen 1990). Since trawling started in the Barents Sea around 1930, annual harvest has been high, with the total harvest from the Northeast Arctic cod stock exceeding one million tonnes per year in several years between 1950 and 1980. With such a high mortality at the feeding grounds, a late-maturing cod will have a low probability of reproducing at all, which will, as our model shows, lead to evolution towards earlier maturation (Law and Grey 1989) and a diminished frequency of skipped spawning.

Consequences of altered exploitation

Our model predicts that exploitation-induced changes in skipped spawning occur on two time scales. On the ecological time scale, exploitation will shift the age distribution of the stock towards younger year classes. The frequency of skipped spawning will therefore increase in the population as a whole, as it is most frequent during the first years after maturation. This is a response at the level of population dynamics (corresponding to a move to the left on the continuous black or shaded curve in Fig. 2). On the evolutionary time scale, a high fishing mortality creates a selection pressure towards earlier maturation. Skipped spawning will then become less common as the stock adapts. This is an evolutionary response to high exploitation rates (a move from the shaded to the black to the dotted curve in Fig. 2). Thus, our model suggests that high fishing pressures will lead to contrasting short-term and long-term effects of exploitation on skipped spawning.

Implications for estimating and using stock–recruit relationships

The frequency of skipped spawning predicted by our model has consequences for stock–recruit relationships whenever the mature part of the population is used to predict recruitment (Jørgensen and Fiksen 2006). Spawning stock biomass (SSB) – recruit models commonly assume that all sexually mature biomass contributes equally to the population's overall egg production. There may be, however, effects of age and experience that modify this, e.g., among first-time spawners (Kjesbu et al. 1996; Trippel 1998; Murawski et al. 2001). Skipped spawning will add on top of this, as its consequences are particularly pronounced for the abundant year classes following maturation. Technically, an inflated value of the SSB will be used inadvertently, as up to 30% of mature individuals may skip spawning in an average year. Moreover, cohorts are affected differently, meaning that cohort abundance and growth history affect skipped spawning in intricate manners. Understanding how these factors influence the part of the population that is actually spawning requires further research, especially observations to determine to what degree the predictions from modelling attempts such as the one presented here apply in nature.

To prevent these distortions in estimated SSB, some measure of individual condition (e.g., lipid stores in the liver) could be used, providing a better estimate of the part of the mature population that has actually prepared for spawning. This could improve predictions for recruitment (Marshall et al. 1999). However, a possible pitfall for such a method is the bimodality in gonad or liver weights that can arise when part of a cohort skips spawning (Schwalme and Chouinard 1999). Different population-level measures were tested as predictors of the stock's total egg production using this

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model (Jørgensen and Fiksen 2006). The population's total liver weight was a good predictor of total egg production, although using the biomass of the part of the population actually engaged in spawning was an even better predictor.

In conclusion, using the age distribution of a stock can increase the explanatory power in both SSB–egg production and SSB–recruit relationships. For such improvements to be realised, the age-specific rates of reproductive success stemming from fecundity, breeding pattern, and egg quality have to be included in predictive models, as well as the age-specific frequencies of skipped spawning. This study supports the view that skipped spawning is such a common phenomenon that it can hardly be neglected in models addressing recruitment. For example, the reproductive potential of exploited cod stocks is often heavily dependent on one or a few strong year classes. However, a large proportion of such a strong year class will reach sexual maturity in the same year, and thus the same large proportion will be likely to skip spawning the following year. Understanding such swings in reproductive potential is particularly important during recovery periods when recruitment is crucial. Further theoretical, experimental, and field research is clearly needed to fully understand the mechanisms regulating the frequency of skipped spawning and to further assess its implications for individual cod and cod stocks as a whole.

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A stochastic approach to stock reduction analysis

Carl J. Walters, Steven J.D. Martell, and Josh Korman

Abstract: Stock reduction analysis (SRA) can complement more detailed assessment methods by using long-term historical catches to estimate recruitment rates needed to have produced those catches, yet still end up with stock sizes near those estimated by the detailed methods. A longer historical perspective can also add information to the estimation of reference points such as unfished biomass (B_0) or target biomass (B_{MSY}). Deterministic SRA models provide a single stock size trajectory that is vanishingly unlikely to have actually occurred, while stochastic SRA attempts to provide probability distributions for stock size over time under alternative hypotheses about unfished recruitment rates and about variability around assumed stock–recruitment relationships. These distributions can be generated with age-structured population models by doing large numbers of Monte Carlo simulation trials and retaining those sample trials for which the stock would not have been driven to extinction by historical catches. By resampling from these trials using likelihood weights (sampling – importance resampling method), it is possible to move into fully Bayesian, state–space assessment modeling through a series of straightforward steps and to provide understandable visualization of how much the data help to reduce uncertainty about historical fishing impacts and stock status.

Résumé : L'analyse de réduction des stocks (SRA) peut être complémentaire des méthodes plus détaillées d'évaluation, car elle utilise les captures à long terme du passé afin d'estimer les taux de recrutement nécessaires pour la production de ces captures, tout en produisant des estimations de la taille des stocks qui se rapprochent de celles obtenues par les méthodes détaillées. Une perspective historique plus étendue donne des renseignements supplémentaires pour l'estimation des points de référence, tels que la biomasse non exploitée (B_0) et la biomasse ciblée (B_{MSY}). Les modèles SRA déterministes génèrent une seule trajectoire de la taille du stock dont l'existence est de moins en moins improbable, alors que les essais SRA stochastiques donnent une distribution de probabilité des tailles du stock en fonction du temps sous diverses hypothèses concernant les taux de recrutement dans des conditions de non exploitation et concernant la variabilité reliée aux relations stock–recrutement présupposées. Ces distributions peuvent être générées par des modèles structurés en fonction de l'âge en faisant un grand nombre d'essais de simulation de Monte Carlo et en retenant les essais échantillons chez lesquels les captures du passé n'auraient pas produit l'extinction des stocks. En échantillonnant de nouveau ces essais à l'aide d'une pondération de vraisemblance (méthode d'échantillonnage – ré-échantillonnage d'importance), il est possible d'aborder une modélisation état–espace pleinement bayésienne par une série d'étapes directes et d'obtenir ainsi une représentation compréhensible du rôle des données dans la réduction de l'incertitude concernant les impacts passés de la pêche et le statut des stocks.

[Traduit par la Rédaction]

Introduction

Stock reduction analysis (SRA) was first suggested by Kimura and Tagart (1982) and Kimura et al. (1984) as a simple method for using historical catch data in conjunction with estimates of relative stock reduction due to fishing to reconstruct possible trajectories of stock decline. In early applications, the main question asked with the method was simply, "How large must the stock have been, and how large must recruitment rates have been over time, in order that historical catches have caused an assumed or observed relative change in stock size?" An ability to answer this question is obviously important for setting fishery reference points and for examining the credibility of estimates of stock–recruitment parameters based on detailed analysis of more recent assessment data (e.g., information on size–age structure).

There has been an unfortunate tendency in recent fisheries assessment work to ignore evidence from long-term catch data with the advent of methods for fitting very complex assessment models to relatively short time series of detailed data. Such assessments might result in highly unreliable or nonsense estimates for recruitment parameters representing how much larger recruitments might have been before fishing. The first author has been involved in two recent assessment cases (red snapper *Lutjanus campechanus* in the Gulf of Mexico and white sturgeon *Acipenser transmontanus* in the Fraser River) where the application of SRA has led to surprising insights about recruitment change (or lack of it) that were not at all evident from more complex analyses; these cases lead us to believe that SRA should be a required assessment component rather than a methodology for use only in data-poor situations. In the red snapper case, detailed assessments have focused particularly on determining the recruitment impact of very large bycatches of ages 0–1 red

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snapper (around 20–30 million juveniles per year, compared with total commercial plus sport landings of 2–3 million older fish per year) by the Gulf of Mexico shrimp fishery. There has been much debate about whether these bycatches have had much additive impact on recruitment, because of the possibility of density dependence in juvenile mortality rates. M. McAllister (Imperial College London, RSM Building, Prince Consort Road, London, SW7 2BP, UK, personal communication) has used SRA to demonstrate that if natural recruitments were much higher (as the application of additive survival models to the bycatch would indicate), the historical fishery would never have substantially impacted the stock (i.e., there is very likely strong density dependence in survival). In the Fraser River white sturgeon case, we have excellent mark–recapture estimates of current stock size (2000–2004) from a large passive integrated transponder (PIT) tagging program (15 581 fish, Nelson et al. (2004)), but these estimates give us no idea of how to set stock recovery goals. Based on simple inspection of historical catch tonnages, which were huge in the late 1800s compared with the 1900s, biologists have generally assumed that the white sturgeon stock is still severely depleted. But SRAs by Echols (1995) and in this paper indicate that in fact the stock was never in any great danger and may be most of the way to fully recovered already. We do not mean to imply by these examples that SRA will always lead to more optimistic assessments than has been conventional wisdom (e.g., do not expect large gains from shrimp bycatch reduction, consider allowing white sturgeon retention fisheries again); the important point is that SRA offers an important, unique way to challenge that wisdom.

In this paper, we first review the relatively simple equations needed to apply deterministic SRA to age-structured population models, so as to account for known historical changes in size and (or) age selectivity of harvesting. Then we demonstrate use of Monte Carlo simulations to generate probability distributions for past stock sizes given alternative hypotheses about mean natural recruitment and variability around average stock–recruitment relationships. We also provide examples of a full Bayesian approach and discuss the relative merits of sampling – importance resampling (SIR) and Markov chain Monte Carlo (MCMC) approaches to samping the posterior distribution. We close by reflecting on the relationship between such SRA methods and full Bayesian state–space methods for stock assessment.

Deterministic age-structured SRA

The essential idea in a generalized stock reduction analysis is to construct a population dynamics model that consists of leading parameters (e.g., R_0 and K in this paper) that describe the underlying production and carrying capacity and subtract known removals from the population over time. (Note that it is the leading parameters that are of general interest in terms of establishing reference points.) Given initial estimates of these leading parameters, the SRA approach then simulates changes in abundance by subtracting estimates of mortality and adding estimates of new recruits, where the new recruits are a function of the current stock size and the leading parameters. Estimates of mortality are based on independent estimates of natural mortality rates, as well as known removals. In short, SRA is carried out by using the historical catch information to drive the population dynamics model forward from a historical reference point near the beginning of the fishery (1880 in the Fraser River white sturgeon case). Therefore, as in all other forms of stock assessments that rely on relative abundance indices, it is absolutely crucial to have historical information on removals or fishing effort and catchability to infer historical changes in abundance and ultimately estimate key population parameters that are essential in defining reference points. The key population parameters of the population dynamics model are then adjusted until the simulations produce numbers near those estimated from independent estimates of absolute abundance (e.g., estimates obtained from tagging studies) or until they produce trends that are similar to trends in relative abundance indices (e.g., catch–effort series). When the model is provided parameter sets that produce population numbers that are too low to have sustained historical catches, it predicts that the population should have disappeared long ago. When the model is provided parameter sets that produce population numbers that are too high, it predicts too little historical fishing impact and a current population size that is too large. So in essence we fit the reconstruction model to historical data just by adjusting key population parameters (i.e., unfished recruitment and recruitment compensation) so as to give a simulated stock history that both incorporates historical fishing impacts and ends up near the current estimates of stock size. Note also that the population dynamics model could also include forward projections beyond the existing time series data and examine alternative future harvest policies.

In this paper, we first fit a deterministic, age-structured SRA model for Fraser River white sturgeon by varying assumed natural recruitment rate or (and) unfished abundance (i.e., leading parameters) so as to maximize the likelihood of the 1999–2004 mark–recapture data (for fish ≥60 cm fork length). That is, the SRA model predicts total abundance for each year, and from these abundances and calculated abundances of marked fish (adjusted for marks added and survival rate from year to year), we predict the number of marked and unmarked fish that should have been captured each year and compare these to the observed numbers using the same Poisson likelihood function as used for the mark–recapture analyses.

For cases like white sturgeon, we recommend starting SRA with a deterministic, age-structured population accounting model in a spreadsheet (e.g., Microsoft Excel, Microsoft Corporation, Redmond, Washington). For white sturgeon, we used an accounting scheme based on Korman and Walters (2001), with 100 ages. Numbers were assumed to change over age a and years t according to the survival equation

$$(1)\qquad N_{a+1,t+1} = N_{a,t}S(1 - v_{a,t}U_t),$$
$$a = 1,\ldots, 100,\ t = 1880,\ldots, 2004$$

where $S = e^{-M}$ is the natural survival rate (mortality rate $M = 0.08\text{-year}^{-1}$) and is assumed constant, $v_{a,t}$ is the relative vulnerability of an age a fish in year t to fishing, and U_t is an estimate of the exploitation rate on fully vulnerable fish ($v_a = 1$) in year t. To drive such models, we need to estimate or predict S (from tagging analysis in the white sturgeon

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case), $v_{a,t}$ from analysis of age and (or) size harvest composition information, the U_t time series, and recruitment rates $N_{1,t}$ for all years after 1880.

For each year, the overall exploitation rate U_t in eq. 1 can be calculated from historical total catches C_t (in kg) as

$$(2) \qquad U_t = \frac{C_t}{\sum_a N_{a,t} v_{a,t} w_a} \qquad \text{except } U_t < 1.0$$

where w_a is the average weight of an age-a fish. The denominator in this equation is the predicted total, vulnerable biomass in year t, summed over all ages a in that year. Note that a good indication of bad $N_{a,t}$ estimates is to have this calculation predict some $U_t > 1.0$ (i.e., historical catches larger than the biomass of fish predicted to have been available).

For cases where historical catches are available for all years by gear types g with assumed vulnerability schedules $v_{g,a,t}$, eqs. 1 and 2 can be replaced with approximations based on assuming $N_{a,t}$ to have been initially available each year to all gears. That means replacing the $v_{a,t}U_t$ term in eq. 1 with a sum over g of $v_{g,a,t}U_{g,t}$ terms, while estimating each gear-specific $U_{g,t}$ using eq. 2 with the $C_{g,t}$ and $v_{g,a,t}$ for that gear.

In the absence of other information about the form of the stock–recruitment relationship, recruitment rates $N_{1,t}$ should be predicted from estimates of annual egg production $E_t = \sum_a N_{a,t} f_a$ (where f_a is relative fecundity at age a) using a Beverton–Holt recruitment relationship. The Beverton–Holt relationship is almost universally seen in empirical fish stock–recruitment relationships (now around 300 cases; Myers and Barrowman 1996; Myers et al. 1999) for reasons reviewed in Walters and Martell (2004). We recommend the compensation ratio or a form of the relationship

$$(3) \qquad N_{1,t+1} = \frac{K(R_0/E_0)E_t}{1 + [(K-1)/E_0]E_t}$$

where R_0 is an unknown parameter (to be estimated) representing the average unfished age-1 recruitment, E_0 is average annual egg production for an unfished population with recruitment R_0, and K is the Goodyear recruitment compensation ratio (see Walters and Martell 2004), representing the steepness of the stock–recruitment curve at low stock sizes as the ratio of juvenile survival rate at low stock to juvenile survival rate in the unfished population. For white sturgeon, we assumed $K = 5$, which is roughly the average value reported for a wide range of populations by Myers et al. (1999). Sensitivity of the historical reconstructions to various (R_0,K) possibilities was explored by varying K from 2.0 (near the minimum observed in other populations) to 1000 and examining how this affected the R_0 estimates.

Historical data sources for the Fraser River white sturgeon case

Semakula and Larkin (1968) provide reconstructions of annual historical white sturgeon catches for 1880–1963, and Echols (1995) has summarized gill net catches for 1953–1991. No retention of white sturgeon in fisheries has been allowed since then, and we estimated mortalities due to gill net bycatch and sport catch–release fishing to be around 15% of annual estimates of catches for these fisheries after 1991. A critical problem in using such estimates for SRA is that the data are typically reported only in weight units, so we must rely upon the model calculations of changes in average body size (see eq. 2) to essentially convert the biomass harvest to numbers of fish killed over time (Fig. 1*b*). These changes are of two types: (*i*) decreases in mean body size in the field population owing to cumulative removal of older, larger fish and (*ii*) effects of gear mix (e.g., hook and line vs. gill nets) on the vulnerability schedules $v_{a,t}$. Based on growth and survival schedules, we would, for example, expect the current recreational vulnerability schedule to result in a mean weight of fish caught of ~35 kg, if the unfished

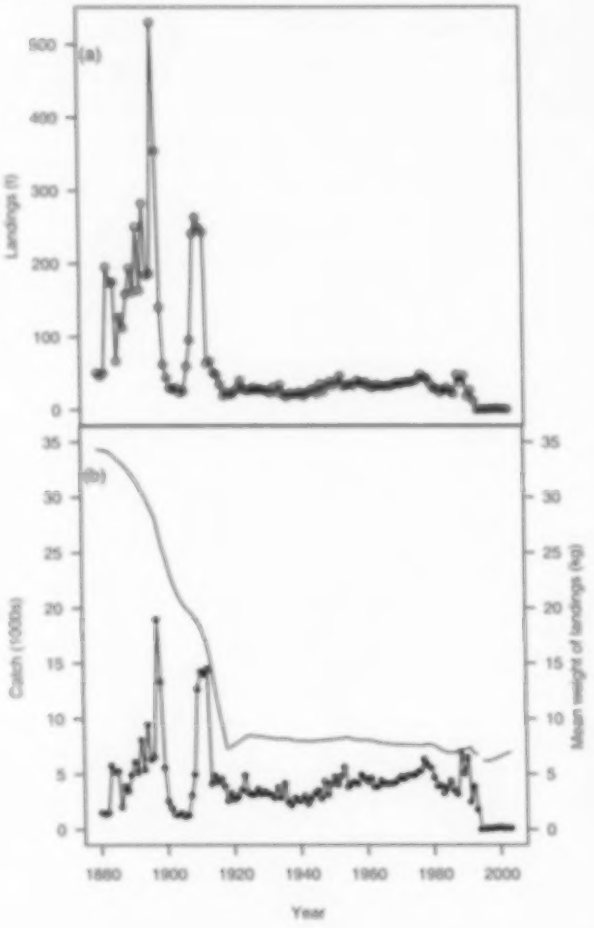

Fig. 1. (*a*) Historical catches (in tonnes) of white sturgeon (*Acipenser transmontanus*) in the Fraser River. (*b*) Catch in numbers (line with dots) were converted from weight by using estimates from population models of average weight of fish (solid line) vulnerable to gears used at different times. Pre-1920 catches were of much larger fish (20+ kg average) than afterward when main catch was by gill nets that take narrow size range (3.3 kg average).

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stock structure (much higher proportions of larger, older fish) were available to that fishery; even with the present eroded age structure, the average weight of fish PIT-tagged in 1999–2004 has been 25 kg. In contrast, the average weight of fish caught by gill nets is ~3.3 kg. That is, the average body weight of fish in the catch may well have declined by a factor of more than 10, implying that the early historical fishery may only have been taking the same number of fish per year as that of the recent (1950–1980) gill net fishery, even when it was taking tonnages 10 or more times as high (Fig. 1*a*).

For years prior to 1900, when targeted commercial fishing used a variety of gears to take white sturgeon of a wide range of sizes, we assumed the same white sturgeon $v_{a,t}$ schedule as estimated for recent recreational harvest sampling by a volunteer PIT tagging program. Since 1920, the bulk of the catch has been gill net bycatch, which selectively takes a narrow range of white sturgeon sizes; using the size data reported in Nelson et al. (2004) and assuming a vulnerability schedule shaped like a normal distribution, we estimated a second $v_{a,t}$ schedule for the post-1920 period. For the 1900–1920 period, we assumed a smooth (linear) shift between the two vulnerability schedules, from 0% to 90% gill net type.

Historical data sources for the Georgia Strait lingcod case

Below, we use a second case study on lingcod (*Ophiodon elongatus*) in the Georgia Strait, British Columbia, to briefly illustrate some difficulties in using SRA for cases where high exploitation rates have resulted in continued stock depletion over long periods. Cass et al. (1990) provide historical reconstructions of annual landings from line and trawl fisheries for lingcod in the Georgia Strait from 1889 to 1985, as well as a review of biological information on age at maturity, growth, and natural mortality. Landings from recreational and commercial fisheries for 1980–2002 and 1986–2002, respectively, were taken from King et al. (2003). A relative abundance index based on commercial and recreational catch per effort in King et al. (2003) was developed for the period 1967–2002. Commercial fisheries for lingcod in Georgia Strait have been closed since 1993, and recently the recreational fishery has seen changes in restrictions, ranging from size limits, seasonal closures, and most recently nonretention of all lingcod. There is limited data on size composition of the historical landings of lingcod; therefore, we assumed that vulnerability schedules were roughly constant over time with age at 50% vulnerability equal to 3.5 years of age.

Baseline deterministic SRA results for Fraser River white sturgeon

A baseline estimate of the lower Fraser River abundance history from SRA is shown (Fig. 2*a*), using the default survival and vulnerability parameter values mentioned above. This history is very similar to that estimated using a simpler (delay-difference) model by Echols (1995). For this estimate, the Beverton–Holt R_0 (unfished natural recruitment, number of 1 year olds per year) was varied so as to give a maximum likelihood estimate of current vulnerable abundance (to recreational fishing) of 40 000 – 60 000 fish and recent trends similar to those obtained from mark–recapture analysis but smoother over time because of the Beverton–Holt recruitment assumption in the SRA calculation (Fig. 3). Assuming compensation $K = 5$, this current abundance required $R_0 = 21\,600$, and the Beverton–Holt model predicts recent (1990s) average annual recruitments of around 7500 yearlings (i.e., about 1/3 of the natural level).

Calculated exploitation rates (U_t) from the baseline scenario (Fig. 2*b*) indicate that the high-tonnage fishery before 1900 (Fig. 1*a*) did not generate very high exploitation rates (the tonnage represented relatively few large fish). Rather, peak commercial exploitation rates are estimated to have occurred during the 1960–1980 period of highest gill net bycatch (Fig. 2*b*).

Stochastic SRA using Monte Carlo simulation

The results shown in Fig. 2*a* are not particularly credible, not just because of uncertainties about M and K, but also because historical recruitment rates were almost certainly variable around the mean relationship predicted by eq. 3. In deterministic SRA models, we calculate a single trajectory of stock sizes over time, essentially asking the question, "If the stock size had unfished recruitment R_0 and historical recruitments exactly equal to the predicted values from a stock–recruitment curve after fishing started, how large would R_0 have to have been in order that the stock would end up at its present estimated size?" Despite knowing that no stock ever exhibits recruitments over time that are always close to a recruitment curve, we hope that answering this question will at least give the expected or most likely trajectory for the stock to have followed. Unfortunately, this is not really a wise question, considering nonlinearities of population dynamics responses to harvest.

A less presumptuous but computationally more difficult question is to ask, "If the stock had average unfished recruitment R_0 and exhibited recruitment over time that varied around a mean recruitment relationship (around a stock–recruitment curve) in a pattern similar to that observed for other populations, how probable is it that stock size would end up at or near the present estimated size?" The essential idea in asking the stock reduction analysis question this way is to recognize that we cannot and need not know how a given stock behaved over time in any precise or even average way. More specifically, we can ask what the probability is of having obtained the observed current population size estimate if the stock (*i*) had mean historical recruitment rate R_0, (*ii*) followed a mean stock–recruitment relationship that passed through R_0, (*iii*) exhibited realistic variation around that relationship, and (*iv*) was subject to observed historical harvest removals. This probability is an integral of the form

$$(4) \qquad P(\hat{N}\,|\,R_0) = \int_N P(N\,|\,R_0)\,P(\hat{N}\,|\,N)\,\mathrm{d}N$$

Here $P(N|R_0)$ is the probability of the stock ending up at size N given R_0 (and a mean recruitment curve with varia-

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Fig. 2. Estimates of historical mature and vulnerable Fraser River white sturgeon (*Acipenser transmontanus*) stock sizes (*a*) and estimated exploitation rates (*b*) from a deterministic stock reduction analysis (SRA) needed to have withstood historical catches and give recent abundance consistent with mark–recapture estimates of abundance. The vulnerable population applies to line fishing gear, where vulnerability increases from zero for fish less than age 5 to full (1.0) at age 15, and mature population is number of age-20+ fish. Note that exploitation rates as proportions of numbers of fish vulnerable to gill net fishing may be unrealistically high for recent years and may reflect an underestimate of the number of fish vulnerable to gill net harvest. Sensitivity of SRA estimates to natural mortality rate $M = 0.08$ (*c*) and recruitment compensation $K = 5$ (*d*) relative to the baseline run are shown.

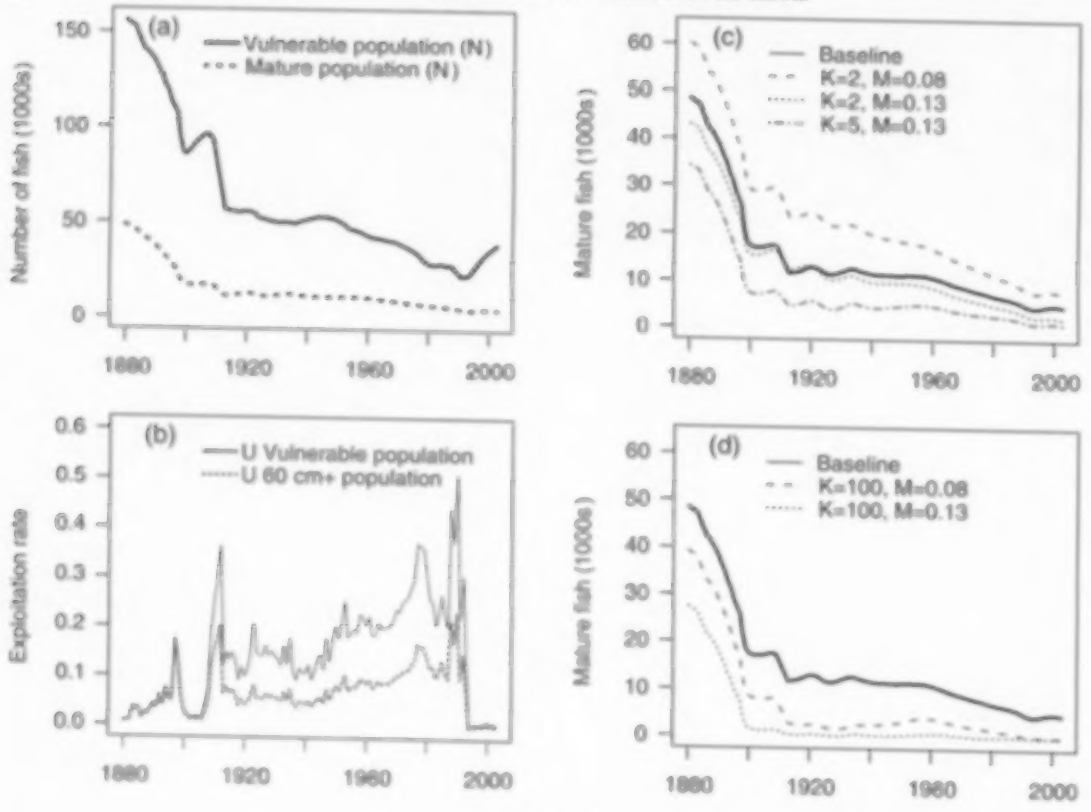
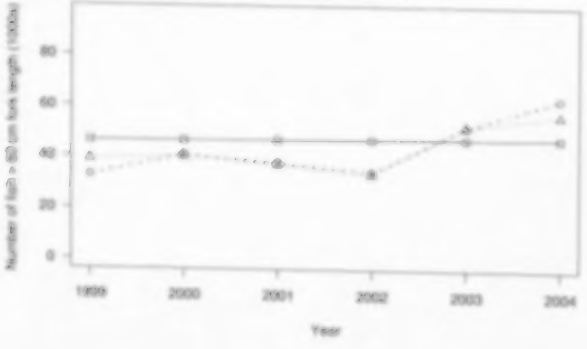


Fig. 3. Comparison of recent abundance of fish ≥60 cm fork length calculated by the deterministic stock reduction analysis model (open squares) with abundances estimated from mark–recapture analyses (open circles and triangles from annual and monthly mark–recapture models, respectively) that did not assume similar recruitment rates from year to year.



tion, and the historical catches), and $P(\hat{N}|N)$ is the probability of obtaining the estimate $\hat{N}$ if the population size were actually N. The second of these distributions, $P(\hat{N}|N)$, is essentially just a likelihood function, representing the odds of obtaining the observed estimate given the true parameter value; we can approximate it simply by assuming normality for the estimator, with some standard deviation. The first, $P(N|R_0)$, is much more complex to calculate.

If we were dealing with a simple population model of the form $N_{t+1} = f(N_t, C_t)$ without complexities in the recruitment prediction due to changes over time in size and (or) age composition and fecundity, a good computational approach to evaluation of $P(N|R_0)$ would be to convert the model into a discrete Markov process with transition matrix $\mathbf{P}(N_{t+1}|N_t - C_t)$ as suggested by Hammond (2004). Unfortunately that approach does not appear to be practical for models with large numbers of state variables (numbers by age). Instead, we must resort to some scheme that involves sampling the probability distributions of past states.

In the sampling approach to estimation of $P(N|R_0)$, we parameterize recruitment variation in some simple way (e.g.,

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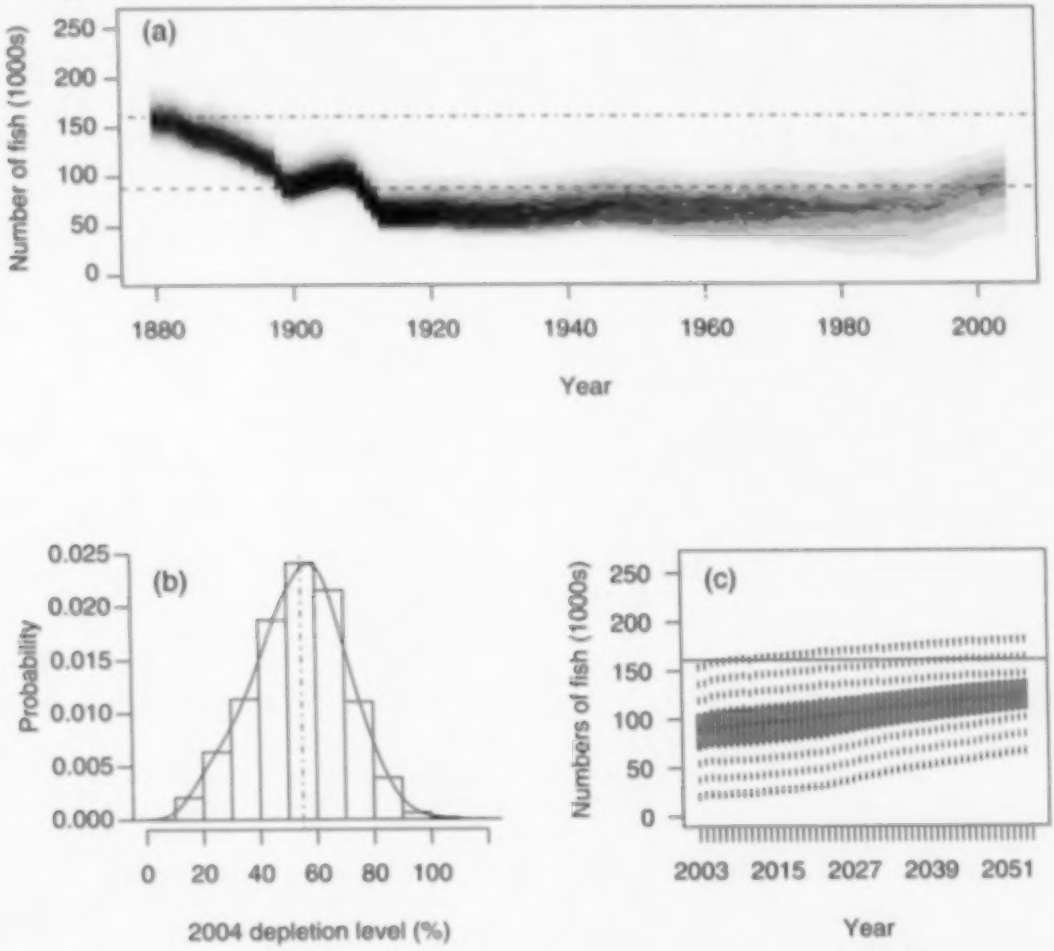
Fig. 4. (*a*) Probability distributions $P(N|R_0)$ for vulnerable stock size (to line fishing) for lower Fraser River white sturgeon (*Acipenser transmontanus*) using stochastic stock reduction analysis. Model run with mean historical recruitment R_0 = 22 000 age-1 recruits, recruitment compensation K = 5. High probability values are shown in darker regions, low values in light regions. (*b*) The median depletion level, calculated as N_{2004}/N_{1880}, is shown by a vertical, stippled line, and the uncertainty is represented by the density. (*c*) Forward projections to 2050 assume total bycatch mortality of 10 000 kg·year^{-1} (around 1000 fish·year^{-1}) by First Nations gill net and recreational fisheries. The upper and lower parts of the box represent 75% and 25% of the scores, respectively. The horizontal line inside the box represents the median. The end of the whiskers represents the largest and smallest values that are not outliers. Outliers are shown above and below the boxes. Note that for this R_0 hypothesis, a high proportion of the simulated recruitment histories resulted in stock extinction.



by annual log-normal multipliers $R_t = f(E_t)e^{w_t}$ on the mean recruitment relationship, so that $N_{1,t} = f(E_{t-1})e^{w_t}$, where E_{t-1} is total egg production the previous year and $f(E)$ is the stock–recruitment equation (eq. 3)). We then choose a large sample of the recruitment anomalies w_t, assuming these to have been sampled from a normal distribution with mean zero and standard deviation σ_R. Each sequence of $T + A$ values (T is the number of years, A is the number of ages) defines a possible population history, where the first Aw_t values in the sequence are applied to the initial age distribution $N_{a,1}$ and the rest to recruitments over time. This approach recognizes that the stock likely had not only variation over the historical fishing period, but also varied in its initial abundance from its very long-term average abundance given mean R_0. When a very large number (e.g., 10 000) of such sequences and simulations have been done, we can approximate $P(N|R_0)$ simply by examining the frequency of N values (binned into suitable sample intervals) over the simulation trials. Note that at least for low R_0 hypotheses, this frequency distribution is not expected to be just smooth and continuous; instead it will have at least some proportion $P(N = 0|R_0)$ of trials where the historical catches are predicted to have driven the stock to extinction (i.e., where stock size is predicted to have been less than the observed catches).

We have developed a simple Visual Basic application to do the sampling approach to estimation of and for age-structured population models. An example of the time probability distributions for stock size generated by this application for the Fraser River white sturgeon example is shown

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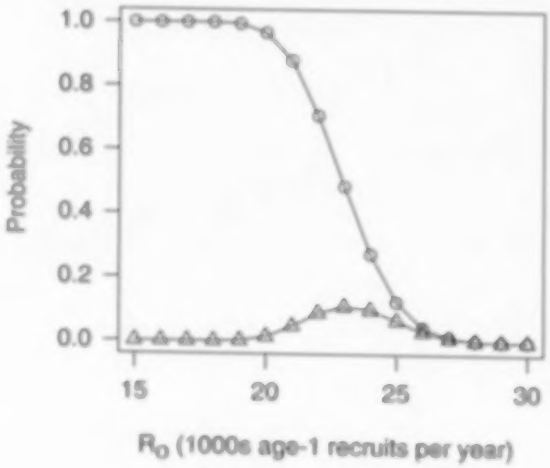
(Fig. 4*a*) for an R_0 case (22 000 annual age-1 recruits) close to that estimated by deterministic SRA. In the development of the application, we included options to for additional sources of variation besides independent random recruitment multipliers: (*i*) we allow for autocorrelation in the recruitment anomalies, with a model of the form $w_t = \rho w_{t-1} + v_t$, with v_t independent; and (*ii*) we allow individual-based binomial sampling of survivals for cohorts that have declined to fewer than N_e individuals (N_e = 1000 by default), so as to represent demographic stochasticity in numbers of larger, older fish (i.e., variation in numbers of fish surviving each year just due to vagaries in the binomial process of individual survival).

Note that the stochastic approach to SRA offers two quite distinct measures for judging the credibility of alternative mean recruitment R_0 hypotheses. One is based only on historical catches and is simply the probability that that stock would have been able to produce those catches without going extinct ($1 - P(N = 0|R_0)$). The other is the overall probability, integrated over possible current population sizes, of producing the observed population estimate (see eq. 4). The second measure will necessarily be low for R_0 hypotheses implying high $P(N = 0|R_0)$, but using it implies a possibly unwarranted trust in our ability to assess uncertainty about the current population estimate (i.e., to specify correctly, which is obviously problematic in the white sturgeon case where the estimate is from mark–recapture methods that may be biased downward because of some proportion of the stock being inaccessible to capture). In the case where recruitment compensation $K = 5$, the probability of extinction for given R_0 hypotheses (i.e., $P(N = 0|R_0)$) approaches 1 for $R_0 \leq 20\,000$ (Fig. 5); note that the results for 10 000 simulation trials are almost indistinguishable from those for 1000 trials.

For the white sturgeon case, it is encouraging that the two credibility measures are in good agreement that the unfished average recruitment rate for lower Fraser River white sturgeon was very probably between 20 000 and 25 000 age-1 fish per year (see Fig. 5). The deterministic SRA gave a most probable value (for explaining mark–recapture results) of around 21 700 fish, about the same as the value that appears most probable from the stochastic analysis that accounts for how a stock with a natural average of fewer than 21 000 fish would have had a high probability (almost 0.5) of being driven extinct by the historical catches. Further, all of the R_0 hypotheses that are even remotely likely to have survived the historical fishery lead to high probabilities that the stock will grow over the next 50 years, so as to approach the unfished level if there is no retention fishery and if bycatch mortalities do not increase.

There are at least two important caveats about results such as Figs. 4 and 5. First, considerably higher variances in population size (and uncertainty about average R_0) are obtained if autocorrelated variation in recruitment residuals w_t is admitted (i.e., if there may have been recruitment regime shifts that caused w_t to behave as autocorrelated with $\rho > 0.4$). Such high ρ values are relatively uncommon in stock–recruitment data sets, but they certainly do occur. Second, small populations such as Fraser River white sturgeon may have considerable variation in abundance of older fish because of demographic stochasticity. Our Visual Basic application allows individual-based sampling of survival for individuals whenever cohort size ($N_{a,t}$) is less than some critical value N_e. When N_e is set to 1000 for white sturgeon (so that we simulate individual survival events for most cohorts by the time they reach mature ages; with annual $S = 0.92$, cohort numbers are essentially deterministic for $N_{a,t} > 1000$), we fortunately do not see noticeably higher variation in vulnerable abundances than shown in Fig. 4.

Fig. 5. Calculated probabilities (from 10 000 simulation trajectories) of extinction before 2004 ($P(N = 0|R_0)$, line with circles) and of having produced recent population estimates of around 50 000 fish (with standard deviation 10 000) vulnerable to angler sampling ($P(\hat{N}|R_0)$, line with triangles) for lower Fraser River white sturgeon (*Acipenser transmontanus*).



Extension to fully Bayesian stock assessment

The basic aim of SRA is to recover information about possible prefishery abundances from historical catches and relatively simple information about recent abundance. But in fact we need not, and probably should not, treat this assessment task as distinct from the more complex models that are typically used to analyze more recent, detailed assessment data. It is actually a relatively minor conceptual and computational step to move from the stochastic SRA approach described here to full Bayesian stock assessment with multiple data sources (catch at age, abundance trend indices, etc.) as recommended, for example, by Maunder and Deriso (2003), McAllister et al. (1994), and Schnute (1994). One popular way to do that would be to (*i*) augment the trajectory sampling procedure to include sampling of other parameters (R_0, K, etc.) along with w_t; (*ii*) choose those parameter samples with a jumping distribution rather than a simple prior for w_t; (*iii*) calculate the likelihood of the data for each trajectory; and (*iv*) use an acceptance rule based on the likelihood to decide whether to include the trajectory in the sample set, instead of including all trajectories for which historical catches would not have caused extinction. After throwing away the early samples (burn in), this would obviously be an MCMC procedure (Gelman et al. (1995), and Fig. 6*a* would

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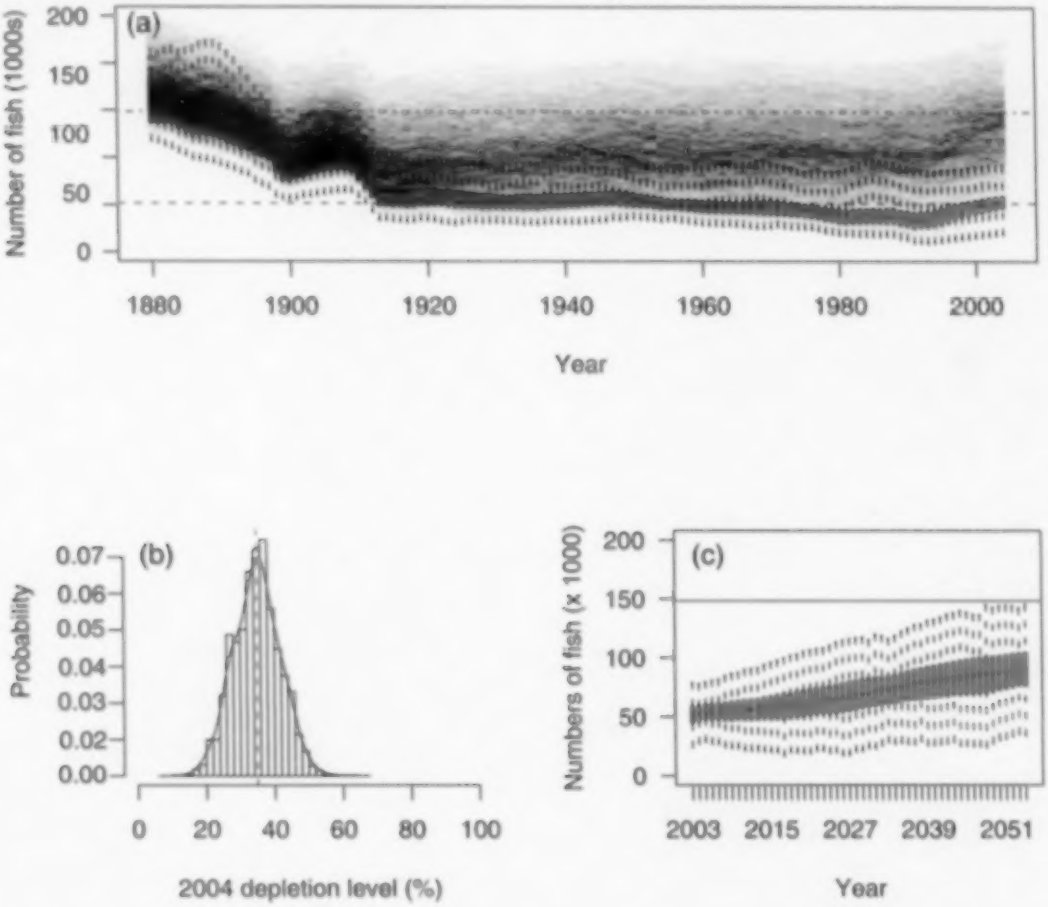
Fig. 6. Impact of a single, tagging-based estimate of current population size on uncertainty about the history of Fraser River white sturgeon (*Acipenser transmontanus*). (*a*) The prior distribution of possible population sizes recognizing uncertainty about recruitment variation and also about parameters of the mean recruitment relationship and survival (R_0, K, S, respectively) is represented, where the darker regions imply higher probability, and the resulting posterior distribution estimated from importance sampling is represented by the box-and-whisker plots. The upper and lower parts of the box represent 75% and 25% of the scores, respectively. The horizontal line inside the box represents the median. The end of the whiskers represents the largest and smallest values that are not outliers. Outliers are shown above and below the boxes. (*b*) Resulting depletion level based on the posterior distribution is shown, and the future projects to 2050 shown (*c*), where the horizontal line represents the median estimate from 1880.



become just a nice way of displaying the posterior distribution of state estimates over time.

But an even simpler and surprisingly informative (and easy to explain to people who are not familiar with stock assessment procedures) way to proceed is to use the SIR procedure recommended by Schnute (1994) and McAllister and Ianelli (1997). That is, (1) augment the sampling of w_t trajectories by sampling also from reasonable prior distributions for leading population parameters (R_0, K) and also uncertain "nuisance" parameters required to calculate likelihoods for complex data (e.g., catchabilities q, selectivity parameters, etc.); (2) calculate the likelihood of the data for each trajectory; and (3) resample from the trajectory set with each element of the set assigned a sample probability proportional to its likelihood (step 3 amounts to using the prior as the importance sampling function). In the case of Fraser River white sturgeon, this greatly reduces the uncertainty in estimates of present day and historical biomass (as denoted by box-and-whisker plots in Fig. 6*a*).

When a graphical scheme like Fig. 6 is used to display and compare the state dynamics results from steps 1 then 3 of the SIR procedure, we can see immediately just how much the data can tell us about the history of fishery impacts. The display from step 1 shows how much uncertainty we would have to admit about that history given only the catch history and prior information about likely parameter values and stochastic variation in recruitment (shaded region in Fig. 6*a*). Then step 2 shows how much that uncertainty is reduced (to a subset of more likely historical trajectories) by weighting each plausible trajectory by its probability of having produced the data. Applying this approach in the white sturgeon case (box-and-whisker plots in Fig. 6*a*), while ad-

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mitting wide uncertainty about R_0 (from 15 000 to 30 000), K (from 2 to 10), and S (from 0.88 to 0.94), demonstrates that having even one relatively certain estimate of current absolute abundance results in a dramatic contraction in the probability distribution for past abundances (compare Fig. 4*b* with Fig. 6*b* and note that fixed values of R_0 and K were assumed in generating the results in Fig. 4).

The steps leading to Fig. 6 are remarkably easy to implement, even with very complex models. First, construct a stochastic population model and a likelihood function for observations given any particular trajectory from this model. Second, run the model in an exploratory or gaming mode to identify plausible ranges for the key recruitment parameters (R_0, K) (i.e., parameter combinations for which the stock would not have been wiped out by observed historical catches and (or) would not have ended up at an unrealistically high present level), perhaps using simple systematic tactics like profiling (as shown in Fig. 5) or searching over grid of R_0 and K values to map out reasonable domains for each parameter. At this point, the typical assessment step would be to fit the model using some nonlinear search procedure to hopefully find a most likely historical trajectory and parameter values. We bypass this step entirely, instead proceeding directly to use of SIR to produce results like the shaded region in Fig. 6*a*. Note that from a statistical perspective, there is nothing wrong with using the second step, which involves analysis of the data, in construction of the parameter prior distributions for the SIR step. This is because all that is being done in the second step is to identify the range of parameter values that are not worth simulating, in the sense that trajectories from these values would be assigned such low likelihood as to never appear in the SIR resample anyway. Put another way, the second step amounts to a very crude approach to adaptive importance sampling (Kinas 1996), using the prior with range restrictions as the importance function.

It is also remarkably easy using the stochastic sampling approach to check for inadequate sampling–resampling and for possible biases in the posterior state sampling due to misspecification of likelihood functions for the data (i.e., of the observation model; e.g., overly optimistic assumptions about variance, structural errors like assuming constant catchability when abundance index data are actually hyperstable). As the first sample state trajectory (from the prior for population parameters and disturbances w_t) is being calculated, replace the assessment data with simulated data generated from either the likelihood functions assumed for the data or more realistically "nasty" assumptions about causes of variation in the data. Then proceed to use these data in calculating likelihoods for every sample trajectory (including the reference true datum) and display the importance resampling results (as in Fig. 6*a*) as though they were real along with the reference state trajectory. If only trajectories far from the reference trajectory are included in the resample, then obviously the assumed likelihood function may be leading to biased results. If only the reference trajectory is included in the resample, then either the initial sample size from the prior (or importance function) is too small, or there is a misspecification of the likelihood function that makes the data appear too informative about the population history. This procedure for replacing the real data can easily be repeated a number of times (different reference trajectory choices) to assure that any findings about bias or misspecification are robust.

When applied to cases where the likelihood function includes much recent data on relative abundance trends and stock composition, it quickly becomes apparent why MCMC sampling procedures have become more popular than SIR. Such data severely restrict particularly the likely recruitment anomaly sequence w_t for recent t, forcing a radical increase in the number of w_t sequences that must be sampled in the initial SIR step so as to have a reasonable sample size for the resampling step. Unfortunately, it is easy to misinterpret this difficulty as evidence that the data precisely determine all uncertain population parameters, including R_0 and K, when in fact these leading parameters may still be highly uncertain except for information provided by the requirement to have sustained long-term catches.

However, there is also a potentially severe technical problem with using MCMC procedures in such cases, particularly when recent relative abundance indices and composition data indicate strong autocorrelation in recruitment residuals over time. In MCMC, we would typically choose each successive parameter sample with probability proportional to the ratio of posterior probabilities (not likelihoods) of each new candidate sample to that for the previous sample. For recruitment anomaly components of the parameter set, this seems to mean just augmenting the log likelihood by the term $-\Sigma v^2/\sigma_v^2$ (assuming $w_t = \rho\, w_{t-1} + v_t$) to represent a normal prior for all values of v_t. But this penalty term causes MCMC to preferentially sample small values of v for time t before any detailed data are available (i.e., to underestimate uncertainty about historical variation in stock size for early years). A simple way to prevent such underestimation is to include a term in the log posterior reflecting knowledge that if the vs are normal, then $\Sigma v^2/\sigma_v^2$ follows a χ^2 distribution, which can be represented by adding the term $(n/2-1)\times \ln(\Sigma v^2/\sigma_v^2) - 0.5\ \Sigma v^2/\sigma_v^2$ (where n is the number of vs admitted to be variable) to the log posterior. Unfortunately, this penalty term can radically reduce the MCMC acceptance rate, forcing severe reduction in MCMC step sizes for v_t sampling and radically increasing the number of samples required to obtain representative mapping of the posterior distribution for historical stock sizes. In our experience, it can easily end up being much more efficient to use the SIR approach.

Another technical problem, where it is difficult for any stochastic sampling procedure, is to discern between depensatory collapse (due to subtracting historical catches as known arbitrary removals over time) versus full stock recovery to higher levels that we believe are actually there. The Georgia Strait lingcod fishery is such an example of how difficult it is to find trajectories that "thread the needle" (Fig. 7). Declining catches since the 1950s (Fig. 7*b*) could be interpreted in at least two ways: either the stock has been continually overfished for the last 50 years and stock size is declining, or fishing mortality rates have declined and stock size is increasing. In this case, we used a catch-per-unit-effort series (1968–2002) to calculate a likelihood for each sample trajectory, and only the tiny subset of trajectories that imply low current stock size (and rapid recovery during recent years) end up being assigned relatively high likelihoods.

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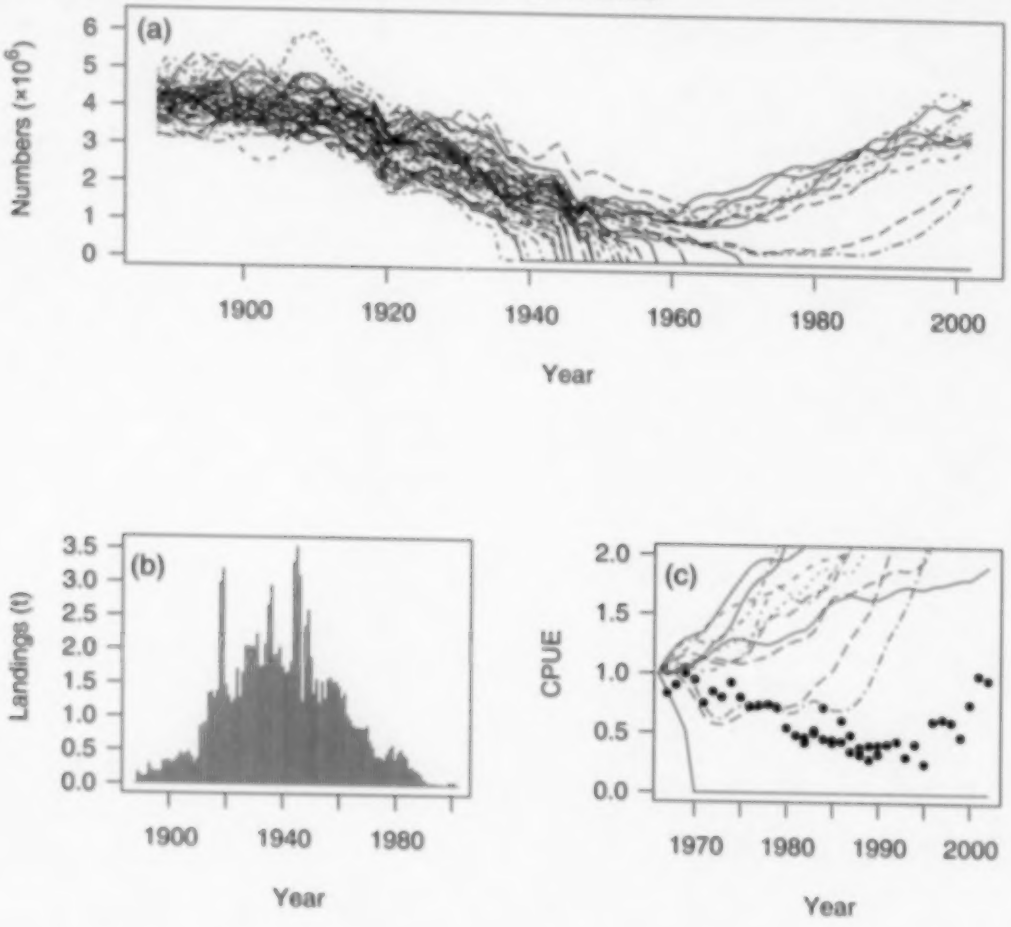
Fig. 7. A sample of 50 possible stochastic stock reconstruction sequences for Georgia Strait lingcod (*Ophiodon elongatus*) (*a*), given the historical catch sequence (*b*). The stock reduction model was run with mean historical, unfished recruitment $R_0 = 1 \times 10^6$ and recruitment compensation $K = 4.0$. Note that a high proportion of the trajectories results in population extinctions prior to 1970 in panel *a*. Panel *c* shows how difficult it is to "thread the needle" between trends in abundance relative to 1967 compared with catch-per-unit-effort (CPUE) data from commercial and recreational fisheries (solid circles).



These trajectories are all associated with low recruitment compensation K values ($K < 4$). To obtain an adequate resample of such trajectories using either SIR or MCMC, we apparently need to generate literally millions of sample trajectories. Obviously, the basic problem in such cases is that it is wrong in the first place to think of the historical catches as having been taken independently of stock size; certainly, they did depend over time on stock size and fishing effort. But without any reliable direct measures of historical fishing mortality rates (or $q \times$ effort), there does not appear to be any alternative but to accept the need to take very large samples of possible trajectories to hit just the few that would generate reasonable mortality rate sequences.

Discussion

In the sections above, we have moved from straightforward SRA population dynamics modeling to some very broad recommendations about how to do stock assessment in general. Nothing that we have presented is in any way original, including even the method in Fig. 6 of visualizing what stock assessments can (and cannot) tell us about historical changes in stock size. If there is a general lesson from the presentation, it is that we need not make stock assessment such a complex and arcane process as it has become in most applications; we can represent and manipulate the population dynamics and statistical likelihood complexities in a series of relatively straightforward steps and can use simple Monte Carlo simulation procedures to integrate those steps. This simple model approach tends to shift the focus to a few key policy parameters that matter rather than obscure obvious polices behind hundreds or thousands of parameters.

One of the key things that we try to estimate using more detailed assessment models and recent size and (or) age composition data is the size or age vulnerability schedule (or commonly, multiple schedules for multiple gear types). When we attempt to reach backward in time to use crude, older historical data to obtain SRA-type perspectives on unfished

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stock size, we obviously have to make some really bold assumptions about how vulnerability schedules might have changed over time because of changes in gear and spatial distribution of fishing. Recall that in SRA, the overall exploitation rate (or rate for a gear type) U_t is estimated as $U_t = C_t / \Sigma_a N_{a,t} w_a v_{a,t}$, where C_t (and perhaps w_a) is known, but $N_{a,t}$ is generated by simulation. In the white sturgeon case, we assume $v_{a,t}$ for $t < 1910$ to have been similar to the v_a that we can estimate from recent line (sport, longline sampling) fishing gears. This leads to high v_a for the fish ages with high w_a and hence to surprisingly low U_t values for the historical fishery despite the relatively large tonnages taken by that fishery. So if we have overestimated historical vulnerabilities for older fish, then we have underestimated historical U_t and the historical impact of fishing on the stock.

So we are left with a nasty dilemma. We can choose not to include the older catch data in assessment because we do not trust the U_t calculations because of uncertainty about $v_{a,t}$. But then we are left with trying to extrapolate unfished abundance from stock–recruitment parameter estimates based on recent data that contain little or no direct information about those parameters, using assessment procedures that are very likely to give biased results (overestimates of K, underestimates of R_0). If we do include the older data, we invite biases due to incorrect specification of historical vulnerabilities along with errors in the estimation of historical catches. These biases may dramatically affect estimates of key population parameters that are used in specifying target reference points.

In the presentation above, we have also failed to address the difficult statistical problem of providing reasonable prior values for, or of estimating, the variance (Σv^2) and autocorrelation (ρ) of recruitment anomalies w_t. These parameters obviously have a big effect on the level of uncertainty admitted about how much historical stock sizes might have varied from any deterministic or average stock size. Much guidance about reasonable values can be obtained by meta-analysis procedures with the Myers recruitment database (www.mscs.dal.ca/~myers/welcome.html), and reasonably precise estimates can sometimes be obtained from detailed assessments based on recent data despite partial confounding of recruitment and observation variances. When in doubt, the simplest strategy is to initially assume the worst (e.g., $\Sigma v^2 > 0.1$, $\rho > 0.6$), then also present results for a few less variable scenarios to determine whether the historical perception of fishery impact would be substantially altered. We suspect that in cases where fisheries impacts are likely to have been severe, such comparative presentations (or admissions of uncertainty about uncertainty) will have almost no impact on perceptions about whether or not current stock size is far enough below unfished levels to warrant substantial policy concern or reaction.

Put another way, it must not be assumed that SRA results can be used as support for particular hypotheses about stock–recruitment parameters R_0 and K. In both the white sturgeon and lingcod examples, it appears possible to conclude that the recruitment compensation K must be relatively low (<5). When higher Ks (steeper recruitment curves) are assumed, even huge ($K > 100$) SIR samples fail to include any trajectories with a low enough current stock size to be considered credible; all trajectories either crash or show fast recovery after the period of peak catches. But in fact, all that the SIR sampling with lower Ks is actually showing is that mean recruitment rates need to have been lower in recent years than the rates needed to have produced historical catches. One way to have obtained such low recruitments is to have had a stationary recruitment relationship with low K. But another entirely plausible way to have obtained low recent recruitments is for the mean recruitment curve to be steep, but to have had nonstationarity involving progressive decline in the R_0 parameter because of habitat or ecosystem changes. Such a model is perfectly plausible for white sturgeon, for which there have been obvious losses of potential juvenile rearing habitat in the Fraser River, and we can certainly find plausible arguments for why potential lingcod recruitment might also have decreased. Such fundamental ambiguities about recruitment stationarity reinforce the argument that stock rebuilding plans must be treated as adaptive management experiments.

In many stock assessments today, detailed recent data provide very precise estimates of current stock size and productivity (recruitment, growth), but not of how large the stock is relative to its unfished state. That information on relative stock size is much more critical to implementation of harvest strategies based on varying exploitation rates in relation to reference points than is information on recent recruitment variation. In these assessments, we are in essentially the same position as for the salmon stock–recruitment example that Walters and Hilborn (1976) and Walters (1986) used in early development of ideas about adaptive control and experimental management. Even in that work, we used a very crude SRA argument by pointing out that early historical catches indicated the possibility of much higher mean recruitment at high spawning stock sizes than was evident from fitting recruitment curves to more recent data. We also had to admit, as must analysts today when examining SRA results for other cases, that historical performance is not always a good guide to the future, in the sense that loss of stock structure and habitat might imply a modern R_0 far lower than the R_0 needed to explain historical catches. We expect that modern SRA procedures will lead to exactly the same debates and to recognition of the need to treat stock rebuilding plans as adaptive management experiments.

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PERSPECTIVE / PERSPECTIVE

Fireproof killer whales (*Orcinus orca*): flame-retardant chemicals and the conservation imperative in the charismatic icon of British Columbia, Canada[1]

Peter S. Ross

Abstract: Long-lived and high trophic level marine mammals are vulnerable to accumulating often very high concentrations of persistent chemicals, including pesticides, industrial by-products, and flame retardants. In the case of killer whales (*Orcinus orca*), some of the older individuals currently frequenting the coastal waters of British Columbia (BC) were born during the First World War, well before the advent of widespread chemical manufacture and use. BC's killer whales are now among the most polychlorinated biphenyl (PCB) contaminated marine mammals in the world. While the "legacy" PCBs have largely been banned, polybrominated diphenyl ethers (PBDEs) have recently emerged as a major concern. The endocrine-disrupting nature of these two persistent fire retardants in biota spells trouble at the top of the food chain, with increasing evidence of effects on reproductive health, the immune system, and development in exposed mammals. The heavy contamination of BC's killer whales, coupled with their long life span and high trophic level, highlights the need for a "weight of evidence" approach in research, conservation planning, and regulatory decisions. Given the global nature of contaminant dispersion, such approaches can only be effective when carried out on both national and international scales.

Résumé : Les mammifères marins qui ont une longue vie et un niveau trophique élevé sont susceptibles d'accumuler des concentrations quelquefois très considérables de produits chimiques persistants, tels que des pesticides, des sous-produits industriels et des retardateurs d'inflammation. Quelques-uns des épaulards (*Orcinus orca*) les plus âgés qui fréquentent les eaux côtières de la Colombie-Britannique (BC) sont nés durant la Première Guerre mondiale, bien longtemps avant la fabrication et l'utilisation répandues de produits chimiques. Les épaulards de BC sont maintenant parmi les mammifère marins les plus contaminés aux biphényles polychlorés (BCP) au monde. Alors que les BCP traditionnels ont en grande partie été interdits, les éthers diphényles polybromés (PBD) sont devenus un sujet important de préoccupation. La propriété qu'ont ces deux retardateurs d'inflammation persistants de perturber le système endocrinien des organismes vivants cause des problèmes au sommet de la chaîne alimentaire; il y a de plus en plus d'indications d'effets sur la santé reproductive, le système immunitaire et le développement chez les mammifères exposés. La forte contamination des épaulards de BC, associée à leur longue vie et à leur position trophique élevée, milite en faveur d'une approche fondée sur le « poids de la preuve » en recherche scientifique, en planification de la conservation et en prise de décisions réglementaires. Étant donné la dispersion des contaminants à l'échelle globale, de telles approches ne seront efficaces que si elles sont employées, tant à l'échelle nationale qu'à l'échelle internationale.

[Traduit par la Rédaction]

Whales, fire, and progress

Fire, and humankind's desire to harness its potential and control its scale, has been a focal point of societies since the advent of civilization. Whale oil, derived from the blubber of baleen and toothed whales, and seal oil, to a lesser extent, provided the combustible fuel for much of the lighting in houses, buildings, and city streets and eventually naviga-

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tional aids and railroad signals in the 16th to the late 19th centuries (Jackson 1978; Bockstoce 1995).

Commercial whaling drove many of the large whale species to the brink of extinction by the late 19th century, with some still struggling to recover today (Gulland 1976; Ross 1993; Baker and Clapham 2004). Over several centuries, the harpoon killed several million cetaceans, as whaling fleets moved from a depleted European and Arctic theatre into the largely uncharted waters of the Pacific and Indian oceans. Simply put, whale oil provided much of western society's illumination as we tapped into the energy stores that whales had accumulated during their lives in the world's oceans. The flammability of whale oil was not only evident in the myriad of lighting practices, but also by the hazards it presented during processing.

> Another class of accidents to which whalemen seem peculiarly liable … is destruction by fire… [Starbuck 1964]

The switch from biological to geological fuels in the 19th century resulted from a combination of factors, including economics, the reliability of product delivery, a waning supply of whales, the Civil War in the US, catastrophic whaling fleet losses resulting from ice conditions in the 1830s and 1870s, and technological progress on several fronts (Bockstoce 1995). Two Canadian discoveries played key roles in transforming the way in which homes and cities were illuminated: the 1846 discovery by Canadian geologist Abraham Gesner of the process that produced kerosene from coal, and the first North American oil well at Oil Springs, Ontario, in 1858 (followed 1 year later by a gusher at Titusville, Pennsylvania). The end of the whaling era had begun.

> … the whales themselves will undoubtedly be grateful for the discovery of oil which is fast superseding that hitherto supplied by themselves [Shipping List, as cited by Bockstoce (1995)]

Household and industrial lighting and heating needs grew at an ever-expanding rate in the 19th and 20th centuries, and with them came the hazards of unwanted fire. Population growth and urbanization, and the ensuing boom in wood frame building construction, provided ample tinder for the multitude of catastrophic fires that destroyed large urban tracts.

> Flames! Flames! Terrible flames!
> How they rise, how they mount, how they fly.
> The heavens are spread with a fierce lurid glare.
> Red heat is filling the earth with air.
> While, mercy! Mercy! We hear the despairing ones cry.
> [portion of song Passing through the Fire about the Great Chicago Fire of 1871 by George F. Root (1871)]

The insatiable demand for lighting, heating, and energy for domestic and industrial development led to the advent of electricity and electrical distribution grids in the early 20th century. Increasing voltage and grid complexity led to the need for an electrical insulation fluid for capacitors and transformers that was heat- and fire-resistant. This created the market foundation for the emergence in 1930 of one of the early global environmental disasters of the 20th century: the commercial development of polychlorinated biphenyls (PCBs) and the subsequent contamination of aquatic food webs the world over.

An estimated 1.3 million tonnes of PCBs were produced worldwide between 1930 and 1993, approximately half of which took place in the US and 97% of which were used in the northern hemisphere (Breivik et al. 2002*a*). Although largely used as heat-resistant oils in electric transformers and capacitors and as industrial-scale hydraulic fluids and lubricants, PCBs were also used in a variety of other minor applications, including specialized lubricants, plasticizers, ink solvents, adhesives, sealants, and lighting ballast (Addison 1986). Approximately 1.4% of global PCB production is thought to have escaped into the environment (Breivik et al. 2002*b*). The toxicity and widespread occurrence of PCBs led to their being banned in Canada and the US in 1977 and in most other industrialized nations in the late 1970s and early 1980s.

With approximately 400 Canadians dying in fires every year and $1.7 billion in direct fire-related losses (International Association for the Study of Insurance Economics 2004), reducing the risk of fires remains to this day a public safety priority. A number of new fire- and heat-resistant and -retardant chemicals were developed either to replace the PCBs in their former applications or to serve in other products or uses. Polybrominated diphenyl ethers (PBDEs) represent one such product, which was developed to resist fire as an additive component in consumer electronics, automobile plastics, foam upholstery in furniture, carpets, and some textiles (Birnbaum and Staskal 2004). PBDEs have been sold as three commercial products (penta, octa, and deca formulations) and have rapidly gained popularity as an effective means to meet fire-control regulations for product flammability from the 1970s onward.

The extensive use of the "lighter" penta- and octa-PBDE products may explain much of the observed environmental contamination, as degrading upholstery or foam may have released PBDE congeners into the environment (Hale et al. 2002). Although these two products were removed from the European market in 1998 and are currently being withdrawn from the North American market, the continued use of the deca-PBDE formulation ensures that PBDE releases into the environment will continue during the 21st century. Although the "heavier" deca-PBDE product (consisting largely of BDE-209) was thought by some to be immobile in the environment and resistant to degradation (Hardy 2002, 2005), recent research would suggest otherwise, raising the spectre of increased exposures in biota as PBDE use continues (Law et al. 2003; Watanabe and Sakai 2003; Hites et al. 2005).

Although the PCBs and PBDEs differ in production histories and applications, they also possess remarkable similarities (Figs. 1*a*, 1*b*). Both consist of two halogenated phenyl rings with up to 209 theoretically possible congeners, and both represent chemical classes that are lipophilic. PBDEs differ from PCBs in the bound halogen (Br for PBDEs and Cl for PCBs) and in the presence of an ether linkage between the two phenyl rings of PBDEs. These chemical features greatly influence their persistence and fate in the environment, their propensity to partition into aquatic food webs, and their relative vulnerability to metabolic elimination by biota. Positive correlations between PCBs and PBDEs in air and in biota support the notion that these two chemical classes share some general anthropogenic source features

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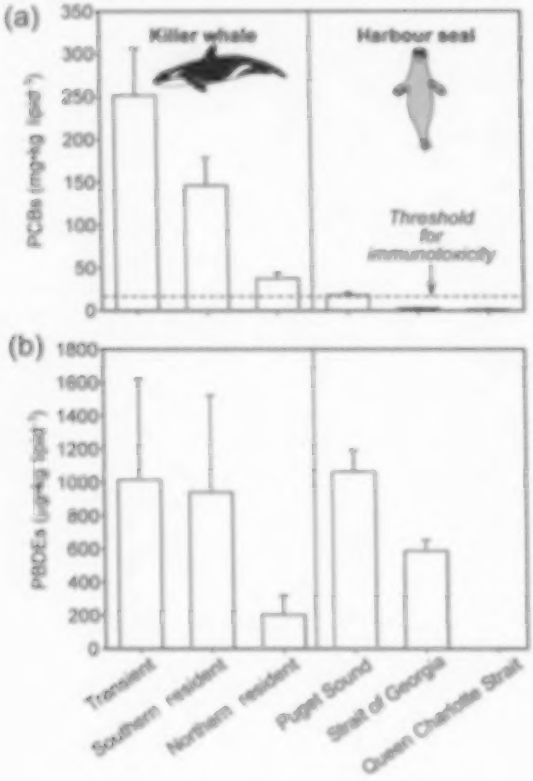
Fig. 1. British Columbia's killer whales (*Orcinus orca*) and harbour seals (*Phoca vitulina*) are exposed to high levels of the regulated polychlorinated biphenyls (PCBs) and moderate levels of the emerging polybrominated diphenyl ethers (PBDEs). (*a*) The "legacy" of the PCBs persists to this day, with British Columbia's killer whales among the most contaminated marine mammals in the world. These killer whales are at risk for PCB-related effects, as their contamination levels easily surpass established toxicity thresholds, including one for immunotoxicity in harbour seals (17 mg·kg^{-1}). (*b*) The exponentially increasing PBDEs levels are found in British Columbia's marine mammals, presenting an emerging health risk to high trophic level biota for the 21st century. (Data from Ross et al. (2000, 2004), Rayne et al. (2004), and P.S. Ross (unpublished data).)



and some of the physico-chemical properties that govern their behaviour in the environment and in aquatic food webs (Manchester-Neesvig et al. 2001; Strandberg et al. 2001).

And while high trophic level marine mammals and other wildlife have been contaminated by often very high concentrations of numerous persistent organic pollutants (POPs), the PCBs and the PBDEs provide an opportunity to evaluate two major contaminant classes of ecotoxicological concern today. With PCBs largely banned but omnipresent as legacy environmental contaminants and PBDEs currently being used, these chemicals provide a contrasting tale of production histories, having both been designed as stable, heat-resistant and fire-retardant products. In fact, the very features that conferred commercial benefits in their slated applications spelled trouble for many marine mammal species, as both PCBs and PBDEs possess congeners that do not readily breakdown in the environment and are amplified in aquatic food chains. Such persistence and bioaccumulative properties are frowned upon by regulators, particularly when the contaminants in question are endocrine-disrupting.

Source, transport, and fate of PCBs and PBDEs in the Northeast Pacific Ocean

The source, transport, and fate of PCBs have been well described in over 30 years of research on Great Lakes, Arctic, and Baltic Sea ecosystems and food webs (Strandberg et al. 1998; Muir et al. 1999; Morrison et al. 2002). The PBDEs are less well understood, although an accumulating literature and a structural similarity to PCBs provide a basis for at least an elementary characterization of source, transport, and fate for these currently used flame retardants (Boon et al. 2002; de Wit 2002; Zhu and Hites 2004).

It is a combination of physical, chemical, and biological functions that drive source, transport, and fate processes, delivering with great efficiency those chemicals that possess certain properties to high trophic level biota. In this way, those contaminants that fall within an optimal physico-chemical "window", namely those with an octanol–water partitioning coefficient ~ log K_{ow} 4.0–7.0, are amplified in food webs (Metcalfe and Metcalfe 1997; Meylan et al. 1999; Christensen et al. 2005). The fundamental processes at the root of contaminant "amplification" in environmental compartments have been described as "solvent switching" and "solvent depletion", reflecting chemical partitioning toward equilibrium in the environment and a solvent-reducing process in biota that retain increasing POP concentrations in lipid stores, respectively (Macdonald et al. 2002).

The octanol–water partitioning coefficients for the PCBs span a lower range (log K_{ow} 4.46–8.18 for PCBs 1 through 209) than their PBDE counterparts (log K_{ow} 4.74–10.33 for PBDEs 1 through 209) (Hawker and Connell 1988; Brackevelt et al. 2003), conferring a slightly different spectrum of interactive properties on the movement of these two contaminant classes in the environment.

Structural differences and a larger molecular mass relative to PCBs is thought to impede heavier PBDE congeners from ready transport across biological membranes and, hence, uptake by biota (Kelly et al. 2004). Although low levels of BDE-209 in aquatic biota would tend to support this notion, detection of relatively high levels of this heavy congener in terrestrial food web dependent Peregrine falcons (*Falco peregrenis*) in Sweden (Lindberg et al. 2004) and Vancouver Island marmots (*Marmota vancouverensis*) and interior grizzly bears (*Ursus arctos horribilis*) in British Columbia (Lichota et al. 2004; Christensen et al. 2005) indicate that it is mobile in the environment, does partition into terrestrial food webs, and is taken up by biota. And, although the highly brominated PBDE congeners (e.g., BDE-209) would tend not to fall within the optimal log K_{ow} window for amplification in aquatic food webs, their debromination, as has been shown in carp (*Cyprinus carpio*), can lead to the formation of lighter congeners (Stapleton et al. 2004) that are

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more mobile and can readily accumulate in aquatic food webs.

The atmosphere plays a key role in the (rapid) dispersion of POPs away from source. PCB and PBDE signatures in sediments and in biota reveal that source regions tend to be "heavier" (i.e., more halogenated) than sink regions (Muir et al. 1996; Ross et al. 2004; Ueno et al. 2004), consistent with the global fractionation processes that favour the transport of the more volatile chemicals into remote regions of the world (Wania and Mackay 2001). Wandering air masses are credited with the delivery of PCBs and other POPs into the Arctic and Antarctic (Risebrough et al. 1976; Muir et al. 1992). Prevailing winds from the west and southwest spread air pollutants across the Pacific Ocean (Blais et al. 1998; Jaffe et al. 1999; Li et al. 2002), with wet and dry deposition of pollutants onto the surface waters of the ocean providing a route of entry into its pelagic food web constituents (Ewald et al. 1998; Guruge et al. 2001; Ueno et al. 2004).

The migratory movements of various fish, birds, and other biota can translocate POPs from one region to another. In the Northeast Pacific Ocean, tens of millions of salmon scavenge food web borne contaminants in the open ocean and deliver these to their natal streams as they return to spawn in Alaska, British Columbia, Oregon, and California. Sockeye salmon (*Oncorhynchus nerka*) were shown to import PCBs from the North Pacific Ocean into Alaskan lakes, introducing not only PCBs into the local watershed and its food web, but also a "heavier" pattern of PCBs that differed markedly from that of the PCB congeners deposited through atmospheric processes (Ewald et al. 1998; Krümmel et al. 2003). We recently attributed 70% of the organochlorine pesticides, 90% of the PCBs, and 85% of the "lighter" PBDEs in coastal (maritime) grizzly bears in British Columbia to their consumption of salmon returning from the Pacific Ocean, highlighting the effectiveness of this biological transport process between marine and terrestrial ecosystems (Christensen et al. 2005).

Several POP classes have been detected in killer whales (*Orcinus orca*) in the Northeast Pacific Ocean, including PCBs, dioxins, furans, organochlorine pesticides, and the flame retardants polybrominated biphenyls (PBBs), polychlorinated naphthalenes (PCNs), and PBDEs (Ross et al. 2000; Ylitalo et al. 2001; Rayne et al. 2004), reflecting net accumulation from ingested prey. Pacific salmon are critical to British Columbia's resident killer whales, comprising an estimated 92% of their annual diet (65% consisting of the long-lived, high trophic level Chinook salmon, *Oncorhynchus tshawytscha*), with the remaining 8% thought to be a mix of other fish, including rockfish (*Sebastes* spp.), lingcod (*Ophiodon elongatus*), halibut (*Hippoglossus stenolepis*), and herring (*Clupea pallasii*) (Ford et al. 1998).

The very high PCB levels and moderate PBDE levels observed in these killer whales are with little doubt due to a combination of what might be described as "local" (via non-salmonid prey) and "global" or "background" (via salmon as prey) sources. Salmon accumulate most of their POP burden at sea, highlighting the potential for a trans-Pacific bridge for contaminant transport (O'Neill et al. 1998). Despite widely cited reports of contaminants in wild Pacific salmon, PCB (~20 μg·kg wet weight^{-1}) and PBDE (~4 μg·kg wet weight^{-1}) concentrations were relatively low in returning 2002 adult Chinook salmon (Hites et al. 2004*a*, 2004*b*) when compared with some of the remaining locally residing killer whale prey items. For example, rockfish species in an urban Puget Sound site had a PCB concentration of approximately 158 μg·kg wet weight^{-1} (West 1997).

These results highlight the potentially skewed importance of locally residing prey items as a contaminant source to resident killer whales. The threefold higher levels of PCBs and fivefold higher PBDE levels in southern resident killer whales compared with their like-eating northern resident counterparts may, in fact, attest to such a local influence, where the southern residents must contend with the industrial coastal waters of southern British Columbia and northern Washington State. Studies of nonmigratory harbour seals (*Phoca vitulina*) (Ross et al. 2004) and their prey (Cullon et al. 2005) support the idea that Puget Sound represents a regional PCB "hotspot" and possible contaminant source to southern resident killer whales.

In addition to proximity to source, the biology and ecology of marine mammals will shape the extent to which they are exposed to POPs. The marine mammal eating transient killer whales are more PCB-contaminated than their fish-eating resident counterparts, reflecting their higher trophic level (Ross et al. 2000). Males are more PCB-contaminated than females, reflecting the transfer of fat-soluble contaminants to offspring via transplacental and lactational transfer to calves. Long lives lead to a long exposure history and a lifetime accumulation scenario, with male killer whales living up to 50 years and females up to 85 years (Olesiuk et al. 1990). And while the metabolic capacities of killer whales and other marine mammals appear to preferentially eliminate dioxin-like compounds, they are less able to eliminate the mono-ortho PCBs and other globular (nonplanar)-structured POPs (Tanabe et al. 1988; De Swart et al. 1995; Ross et al. 2000). Little is known about the metabolic ability of marine mammals towards PBDEs, but a lack of sex-based differences may reflect a reduced reproductive transfer by females to their offspring or nonsteady state environmental (dietary) conditions as PBDE concentrations continue to increase in long-lived marine mammals (Lebeuf et al. 2004; Rayne et al. 2004).

Effects of PCBs and PBDEs on killer whale health

Four major factors impede the direct documentation of causal relationships between exposure to environmental contaminants and adverse health effects in marine mammals: (*i*) the abundance of potentially toxic chemicals that have been detected at often high concentrations in marine mammals; (*ii*) the many natural confounding factors that can complicate interpretation of both contaminant concentrations and health end points in marine mammals, such as age, sex, condition, diseases, reproductive cycles, and stress; (*iii*) the many anthropogenic factors that can influence the health of marine mammals other than endocrine-disrupting contaminants, including biological pollution (pathogen transfer), fishing pressures (reduction of prey base), noise and disturbance, and climate change; and (*iv*) the often insurmountable

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legal, ethical, or logistical challenges associated with obtaining samples from large mammals in an aquatic or semi-aquatic environment.

However, the conserved nature of many physiological end points does provide a foundation for interspecies extrapolation among vertebrates, where laboratory rodents often serve as a basis for the evaluation of risks to humans of a given chemical (Descotes 2003). Similarly, extrapolation and a "weight of evidence" approach provides a basis for characterizing the risk of contaminant-related adverse health effects in marine mammals and enables a compilation of data from studies using in vitro cell culture techniques, laboratory animal models, captive feeding experiments of a marine mammal cohort, and field research using biomarkers or epidemiology (Ross 2000). While extrapolation among species provides an opportunity for a more all-encompassing weight of evidence, observations must incorporate possible interspecies differences in sensitivity to the effects of a given chemical (Hahn 1998).

The dichlorodiphenyltrichloroethane (DDT)-associated eggshell thinning and extirpation of fish-eating birds from large tracts of North America and Europe in the 1960s and 1970s is with little doubt the best-described example of population-level impacts of a single chemical in a wildlife species. The mechanism underlying this occurrence was ultimately resolved through a combination of field and captive dosing studies (Hickey and Anderson 1968; Wiemeyer and Porter 1970; Lundholm 1997). Documenting the health-related impacts of other POP classes has been more challenging, reflecting the highly complex mixtures to which free-ranging animals are now exposed and the multiple levels of possible effects.

At such high concentrations in British Columbia's killer whales, the PCBs are perhaps the most troubling of contaminants in terms of toxicological risk (Ross et al. 2000). The toxicity of PCBs is multifaceted but can be functionally grouped into "dioxin-like" and "non-dioxin-like" mechanisms of action. The former mechanism involves binding of the planar and mono-ortho PCB congeners to the aryl hydrocarbon receptor (AhR) in vertebrates (Hahn 1998), which leads to induction of certain enzymes and a number of effects, perhaps most notably immunotoxicity. The latter group of mechanisms comprises a suite of effects, including the PCB metabolite associated disruption of thyroid hormone (thyroxine) and vitamin A through a competitive binding to their shared transport complex in circulation (primarily transthyretin – retinol binding protein or TTR–RBP) (Rolland 2000; Simms and Ross 2001).

The larger molecular mass and shape of PBDEs are thought to reduce binding affinity to the AhR such that the risk of dioxin-like effects attributed to PBDEs is more limited than those attributed to their PCB counterparts (Chen et al. 2001). However, as with the PCBs, PBDE metabolites appear to be potent competitors for thyroxine in circulation, where they displace this hormone from its carrier complex (Meerts et al. 2000) or increase elimination via upregulation of phase II uridinediphosphate-glucuronosyltransferase (UDGPT) enzyme activities (Zhou et al. 2001). In addition, there is evidence for other endocrine-disrupting influences for both PBDE parent congeners and some of their metabolites, including estrogenicity (Meerts et al. 2001).

In short, both PCBs and PBDEs can, through their parent congeners and their metabolites, alter thyroid and vitamin A economy and affect neurological development, reproductive development, and immune function in exposed mammals (Meerts et al. 2001; Hallgren and Darnerud 2002; Kuriyama et al. 2005). While both similarities and dissimilarities have been observed in the mechanisms of toxic injury between PCBs and PBDEs, more research is needed to reveal the extent to which the documented toxicological mechanisms for PCBs provide a basis for characterizing the risk of toxicity associated with the less documented PBDEs.

While laboratory animal studies provide an important mechanistic basis for assessing toxicological effects attributable to particular chemicals, they do not fully capture the "real world" (complex mixture) exposure scenarios of marine mammals. In two captive studies, harbour seals fed fish caught from more POP contaminated waters caused reproductive impairment and immunotoxicity (Reijnders 1986; De Swart et al. 1994; Ross et al. 1996). In addition, circulating vitamin A and thyroid hormone concentrations were reduced in the exposed seals (Brouwer et al. 1989; De Swart et al. 1994). PCBs represented the dominant POP in these studies, and laboratory rats exposed to the same contaminant profiles provided additional evidence of a PCB involvement in the effects (Ross et al. 1997).

Evidence from the field comes in part from observations of abnormalities in marine mammal populations inhabiting contaminated coastal regions, including skeletal malformations, adrenal lesions, and reproductive impairment in Baltic Sea harbour, ringed (*Phoca hispida*), and grey (*Halichoerus grypus*) seals (Helle et al. 1976; Mortensen et al. 1992; Olsson et al. 1994). Elevated POP concentrations in harbour porpoises (*Phocoena phocoena*) that died from infectious diseases compared with those that died from trauma suggests that contaminant-associated immunotoxicity is affecting immunocompetence (Jepson et al. 1999). A lack of recovery in the contaminated St. Lawrence beluga whales (*Delphinapterus leucas*) (since the 1962 protection of this population), in combination with observations of disease-associated mortalities, has been partly attributed to POPs and other environmental contaminants (De Guise et al. 1995; Lebeuf et al. 2004).

In addition, field evidence derived from correlations between POP concentrations and a number of end points provides important linkages between the field and more controlled laboratory or captive study scenarios. For example, as observed in some captive feeding and laboratory animal studies, contaminant-associated alterations have been observed in a number of marine mammal populations, including alterations in thyroid hormone and vitamin A (Simms et al. 2000; Jenssen et al. 2003; Braathen et al. 2004), cytochrome P450 enzymes (Nyman et al. 2003), and immune function (Lahvis et al. 1995; Levin et al. 2005). In most cases, confounding factors have been eliminated through study design or by statistical means, but critical evaluation of the "correlation" is needed to ensure that the relationship is causal (Ross et al. 2003; Ross 2004).

Carrying out toxicological studies in free-ranging killer whales is fraught with the obvious challenges listed above. However, despite the lack of mechanistic evidence relating the high POP levels in British Columbia's killer whales to an

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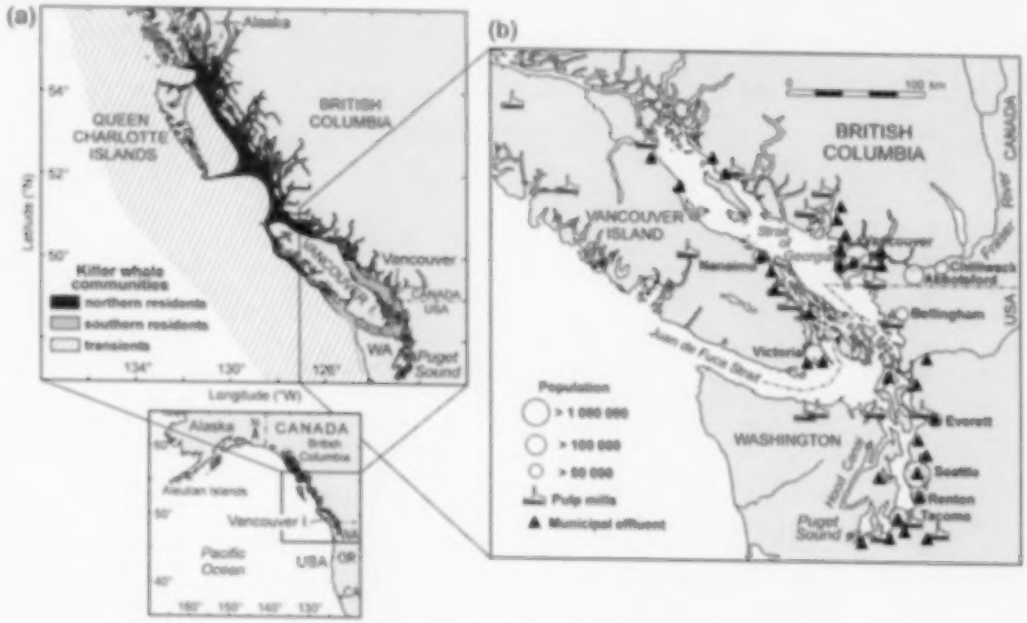
Fig. 2. British Columbia's reproductively isolated killer whale (*Orcinus orca*) communities include the marine mammal eating transients (threatened) and the fish-eating northern (threatened) and southern (endangered) residents (Ford et al. 1998). During their summer feeding season (May–October; see panel *a*), the approximately 89 members of the southern resident community frequent the relatively industrialized Georgia Basin – Puget Sound (see panel *b*), where they feed on returning salmon and can also feed on locally contaminated prey.



observable adverse health effect, there is reason for concern (see Fig. 1). Contaminant-related disruption of several end points in free-ranging harbour seals in local killer whale habitat indicates that POP levels are of biological concern in the coastal food chains of British Columbia and Washington State. In addition, PCB concentrations in northern resident, southern resident, and transient killer whales readily exceed established thresholds for effects of PCBs on reproduction in harbour seals (25 $mg \cdot kg^{-1}$) (Boon et al. 1987) and river otters (*Lontra canadensis*) (7.5 $mg \cdot kg^{-1}$) (Kihlstrom et al. 1992), immune function in harbour seals (17 $mg \cdot kg^{-1}$) (De Swart et al. 1994; Ross et al. 1995), and endocrine effects (thyroid hormone and vitamin A) in river otters (4 $mg \cdot kg^{-1}$) (Smit et al. 1996) and harbour seals (17 $mg \cdot kg^{-1}$) (De Swart et al. 1994; Ross et al. 1995). Extrapolation and a weight of evidence approach therefore imply a significant health risk associated with current PCB burdens in British Columbia's killer whales communities.

Fireproof killer whales and the quest for habitat protection

British Columbia's killer whales face a number of conservation threats. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has listed the southern resident killer whales as "endangered", the northern residents as "threatened", and the transients as "threatened" under the terms of the Species at Risk Act (SARA). The southern residents face three major conservation concerns: (*i*) noise and disturbance associated with heavy vessel traffic; (*ii*) reduced availability of preferred prey (Chinook salmon) because of habitat loss, fishing pressures, and climate change; and (*iii*) high levels of endocrine-disrupting contaminants, such as PCBs (Environment Canada 2005). Each of these is thought to present a real risk to the health and viability of the reproductively isolated southern resident killer whales, such that the SARA-enlisted recovery strategy must address a daunting set of tasks. An initial assessment of the southern resident killer whale community revealed a reduced annual population growth rate compared with that of its northern counterpart (1.3% compared with 2.9%; Olesiuk et al. 1990), which could be due to higher POP concentrations, food limitation, and (or) disturbance from boats. Each of these three stressors on their own can be viewed as a health risk (Ross et al. 2000; Erbe 2002; Williams et al. 2002), but the combination of all three could threaten population viability.

Resident killer whales are heavily exposed to POPs through the consumption of prey such that their habitat might be generically viewed in terms of "local" and "global" sources of contamination. Local habitat for the southern resident killer whales can be described as the area frequented by the approximately 89 individuals of J, K, and L pods during their summer feeding season (~May through October; see Fig. 2*a*; Ford et al. 2000). Identifying killer whale prey species that reside in this region and working towards targets for prey tissue contaminant concentrations that would protect killer whales from adverse health effects represents an important local (regional) mitigative strategy. This area, the Georgia Basin – Puget Sound transboundary region, is at the

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Table 1. While source controls and regulatory efforts led to rapid initial declines in polychlorinated biphenyl (PCB) concentrations in biota, the largely unregulated polybrominated diphenyl ethers (PBDEs) are increasingly exponentially in fish, seabirds, and marine mammals in British Columbia (BC), Canada, and Washington State, USA.

Contaminant	Change (%)	Species	Site	Time frame	Reference
PCBs	–73	Double-crested cormorant eggs	Strait of Georgia	1970–1985	Elliott et al. 1989
PCBs	–92	Harbour seals	Puget Sound	1972–1997	Calambokidis et al. 2001
PBDEs	1200	Mountain whitefish	Columbia River (BC)	1992–2000	Rayne et al. 2003
PBDEs	3640	Great blue heron eggs	Vancouver	1983–2002	Elliott et al. 2005
PBDEs	6950	Harbour seals	Puget Sound	1984–2003	P.S. Ross, unpublished data

Note: Double-crested cormorants, *Phalacrocorax auritus*; harbour seals, *Phoca vitulina*; mountain whitefish, *Prosopium williamsoni*; great blue herons, *Ardea herodias*.

receiving end of emissions and waste discharges from the activities of 7.5 million human inhabitants (see Fig. 2*b*). On the global scale, the growing Pacific Rim economies ensure that contaminants from as many as 2 billion humans will enter the North Pacific Ocean via direct or indirect means. While daunting, working towards the enactment of the Stockholm Convention, which provides a global framework for phasing out the top 12 POPs (including PCBs), and adding the PBDEs to this protocol would serve to protect remote aquatic food chains from contamination and help protect high trophic level wildlife.

Source control and regulatory efforts can be effective at reducing inputs of POPs into local killer whale habitat, as evidenced by temporal trend profiles in biota. The PCBs and PBDEs provide a contrasting picture of contamination by flame-retardant chemicals (Table 1). Although source controls and regulations led to a sharp drop in PCBs in Puget Sound harbour seals during the 1970s and 1980s (Calambokidis et al. 2001), currently used PBDEs have been increasing exponentially in biota from the Great Lakes (Zhu and Hites 2004), the Arctic (Ikonomou et al. 2002), and British Columbia (Rayne et al. 2003; Elliott et al. 2005). Although PCBs remain the top-ranked POP class in coastal food webs in the Puget Sound and Georgia Basin (as documented in composite "food baskets" for harbour seals), PBDEs were second- and third-ranked in these two basins, respectively (Cullon et al. 2005). With the continued use of deca-BDEs in Canada and the US, their degradation into more mobile and bioaccumulative forms, and their doubling time of 3–5 years observed in the environment, PBDEs are slated to become one of the pre-eminent POPs of the century.

Conclusions

The killer whale habitat in British Columbia is changing, reflecting the arrival of European and Asian hunters, whalers, and fishers in the 18th and 19th centuries and the rapid subsequent colonization of the region. Local habitat is noisier, busier, and more contaminated, and the North Pacific Ocean is warmer and increasingly viewed as a sink for environmental contaminants from a rapidly developing Asian economy. Protecting the killer whale food chain must be central to conservation efforts such that contaminants of concern to either the health of salmon or the health of resident killer whales are identified and mitigative measures adopted.

Contaminant source, transport, and fate functions will not remain static; in an ocean where warmer waters and "fishing down the food chain" have altered food web structure, contaminant pathways are likely to change, posing immense challenges to those attempting to study or mitigate contaminant concerns (Pauly et al. 1998; Schindler 2001; Macdonald et al. 2003).

The demand for a fuel source for lighting in the past resulted in the depletion of the world's large cetaceans and a conservation dilemma that persists to this day. It is perhaps ironic that the whale blubber used historically to fuel the flames of our lights is now contaminated with chemicals that were designed to prevent the unwanted ignition and spread of fire.

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The author is responsible for verifying each reference against the original article. Each reference must be cited in the text using the surnames of the authors and the year, for example, (Walpole 1985) or Green and Brown (1990). Depending on the sentence construction, the names may or may not be in parentheses, but the year always is. If there are three or more authors, the citation should give the name of the first author followed by et al. (e.g., Green et al. 1991). If references occur that are not uniquely identified by the authors' names and year, use *a*, *b*, *c*, etc., after the year, for example, Green 1983*a*, 1983*b*; Green and Brown 1988*a*, 1988*b*, for the text citation and in the reference list.

Uniform reference locators (URLs) or digital object identifiers (DOIs) are useful in locating references on the World Wide Web, and authors are encouraged to include these; they should be added to the reference in the reference list (see example below).

Unpublished reports, private communications, and In press references

References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings are not cited in the reference list but may be included as footnotes or in parentheses in the text, giving all authors' names and initials. For a private communication, year of communication should also be given (e.g., J.S. Jones (personal communication, 1999)). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. If an unpublished book or article has been **accepted for publication**, include it in the reference list followed by the notation "In press". Do not include volume and page number in an in-press reference, as these are subject to change before publication.

Presentation of the list

The **reference list** must be double-spaced and placed at the end of the text. References must be listed in alphabetical order according to the name of the first author and not numbered. References with the same first author are listed in the following order. (*i*) Papers with **one author only** are listed first in chronological order, beginning with the earliest paper. (*ii*) Papers with **dual authorship** follow and are listed in alphabetical order by the last name of the second author. (*iii*) Papers with **three or more authors** appear after the dual-authored papers and are arranged chronologically.

General guidelines on references

References should be selected judiciously and be largely restricted to significant, published literature. References should follow the form used in current issues of the Journal. The names of serials are abbreviated in the form given in *Chemical Abstracts Service Source Index* (*CASSI*) (Chemical Abstracts Service, 2540 Olentangy River Road, P.O. Box 3012, Columbus, OH 43210-0012, USA) or in *BIOSIS Serial Sources* (BIOSIS, 2100 Arch Street, Philadelphia, PA 19103-1399, USA). In doubtful cases, authors should write the name of the serial in full. The Journal encourages the inclusion of issue numbers which should be placed in parentheses after the volume number. The following bibliographic citations illustrate the punctuation, style, and abbreviations for references.

Examples of references types, including electronic references

Journal article with DOI:

Newbury, M.G., and Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to

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climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. doi:10.1139/F04-113.

Journal article with URL:

Newbury, M.G., and Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. Available from http://pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_e?cjfas_f04-113_61_ns_nf [accessed 28 October 2005].

Journal article available online only (with DOI):

van der Sanden, J.J., and Hoekman, D.H. 2005. Review of relationships between grey-tone co-occurrence, semivariance, and autocorrelation based image texture analysis approaches [online]. Can. J. Remote Sens. **31**(3): 207–213. doi:10.1139/rs03-011.

Entire issue of journal:

Gordon, D.C., Jr., and Hourston, A.S. (*Editors*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(Suppl. 1).

Report:

Sanders, W.W., Jr., and Elleby, H.A. 1970. Distribution of wheel loads in highway bridges. National Cooperative Highway Research Program Report 83, Transportation Research Board, National Research Council, Washington, D.C.

Book:

Williams, R.A. 1987. Communication systems analysis and design. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Book in a series:

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Part of book:

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. McNeil and D.C. Himsworth. Oregon State University Press, Corvallis, Oreg. pp. 203–229.

Paper in conference proceedings:

Whittaker, A.A., Uang, C.-M., and Bertero, V.F. 1990. Experimental seismic response of steel dual systems. Proceedings of the 4th U.S. National Conference on Earthquake Engineering, Palm Springs, Calif. Vol. 2. pp. 655–664.

Institutional publications and pamphlets:

Dzikowski, P.A., Kirby, G., Read, G., and Richards, W.G. 1984. The climate for agriculture in Atlantic Canada. Available from the Atlantic Advisory Committee on Agrometeorology, Halifax, N.S. Publ. ACA 84-2-500. Agdex No. 070.

Corporate author:

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, D.C.

Thesis:

Keller, C.P. 1987. The role of polysaccharidases in acid wall loosening of epidermal tissue from young *Phaseolus vulgaris* L. hypocotyls. M.Sc. thesis, Department of Botany, The University of British Columbia, Vancouver, B.C.

Web site citation:

Quinion, M.B. 1998. Citing online sources: advice on online citation formats [online]. Available from http://www.worldwidewords.org/articles/citation.htm [accessed 20 October 2005].

Translation:

Koike, A., and Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. [Translated from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983.]

Tables

Tables must be typed on separate pages, placed after the list of references, and numbered with Arabic numerals in the order cited in the text. The title of the table should be a concise description of the content, no longer than one sentence, that allows the table to be understood without detailed reference to the text. Column headings should be brief, but may be amplified by footnotes. Vertical rules should not be used. A copy of the Journal should be consulted to see how tables are set up and where the lines in them are placed. Footnotes in tables should be designated by symbols (in the order *, †, ‡, §, ||, ¶, #) or superscript lowercase italic letters. Descriptive material not designated by a footnote may be placed under a table as a **Note**. Numerous small tables should be avoided, and the number of tables should be kept to a minimum.

Figure captions

Figure captions should be listed on a **separate page** and placed after the tables. The caption should informatively describe the content of the figure, without need for detailed reference to the text. Experimental conditions should not be included, but should be adequately covered in the Methods. For graphs, captions should not repeat axis labels, but should describe what the data show. A single caption can be provided for multipart (composite) figures, with necessary details on the separate parts, identified by their individual labels. If the separate parts require enough information to warrant separate captions, then the composite should be separated into individual figures.

Appendices

An appendix should be able to stand alone, as a separate, self-contained document. Figures and tables used in an appendix should be numbered sequentially but separately from those used in the main body of the paper, for example, Fig. A1, Table A1, etc. If references are cited in an appendix, they must be listed in an appendix reference list, separate from the reference list for the article. If there is more than one appendix, label as follows: Appendix A, Appendix B, etc.

Supplementary material

Supplementary material (or data) consists of extra tables, figures (maps), detailed calculations, and data sets produced

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by the authors as part of their research, but not essential for understanding or evaluating the paper, and not published with the article in the print edition of the Journal. Depending on the policy of the Journal, such material may or may not be peer reviewed with the article. Supplementary material should be submitted with the article. During Web submission (OSPREY), relevant files should be attached under "Supplementary data". For mail submission, supplementary material should be clearly marked as such. The National Research Council of Canada maintains a depository in which supplementary material may be placed, either at the request of the author or at the suggestion of the Senoir Editor. In addition, supplementary material can now be made available in its native file format on the Journal Web site. It will be linked from the Web page of the associated article. Tables and figures should be numbered in sequence separate from those published with the paper (e.g., Fig. S1, Table S1). The supplementary material should be referred to in the printed article by footnotes. Copies of material in the depository may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Computer programs

It is not the policy of the Journal to publish detailed printouts of computer program statements. Where the availability of these details enhances the usefulness of the paper, the author should submit two copies of the program for deposit (see Supplementary material section).

Illustrations

General

One original and two copies of figures must be submitted to the Editorial Office, even if electronic versions are to be submitted for use in production.

Each figure or group of figures should be planned to fit, after appropriate reduction, into the area of either one or two columns of text. The maximum finished size of a one-column illustration is 8.6 × 23.7 cm (3.4 × 9.3 in.) and that of a two-column illustration is 18.2 × 23.7 cm (7.2 × 9.3 in.). The figures (including halftones) must be numbered consecutively in Arabic numerals, and each one must be referred to in the text and must be self-explanatory. All terms, abbreviations, and symbols must correspond with those in the text. Only essential labelling should be used, with detailed information given in the caption. For **hard-copy versions**, each illustration must be identified by the figure number and the authors' names on the back of the page or in the left-hand corner, well away from the illustration area.

Line drawings

All lines must be sufficiently thick (0.5 points minimum) to reproduce well, and all symbols, superscripts, subscripts, and decimal points must be in good proportion to the rest of the drawing and large enough to allow for any necessary reduction without loss of detail. Avoid small open symbols; these tend to fill in upon reproduction. **Lettering produced by dot matrix printers or typewriters, or by hand, is not acceptable.** The same font style and lettering sizes should be used for all figures of similar size in any one paper. Original recorder tracings of **NMR, IR, ESR spectra,** etc., are not acceptable for reproduction; they must be redrawn. For **hard-copy versions**, line drawings should be made with black ink or computer-generated in black on high-quality white paper or other comparable material; laser prints should be created at the highest resolution available.

Maps

Maps must have very **clear, bold patterns** and must show longitudes and latitudes (or UTM coordinates) and a scale, to ensure proper identification of study locations. On **maps of Quebec**, the official name of municipalities must be used (e.g., Québec, Montréal, Clarke City) and physical features must be in French (e.g., Lac Bienville) except for those that are considered of pan-Canadian significance. Areas of pan-Canadian significance have an official form in English and French (e.g., Atlantic Ocean and Océan Atlantique) and should appear in the language of the paper. Quebec (the province) must also appear in the language of the paper. For a complete list of names of areas of pan-Canadian significance, see pp. 236–237 of *Le guide du rédacteur* (2nd ed., 1996), published by Public Works and Government Services Canada, Ottawa, ON K1A 0S5.

Photographs

Photographs should be continuous tone, of high quality, and with strong contrast. Only essential features should be shown. A photograph, or group of them, should be planned to fit into the area of either one or two columns of text **with no further reduction**. Electron micrographs or photomicrographs should include a scale bar directly on the print. The best results will be obtained if the authors match the contrast and density of all figures arranged as a single plate. **Hard-copy versions** must be printed on glossy paper and be trimmed and mounted on **thin** flexible white bristol board with no space between those arranged in groups.

Colour illustrations

Colour illustrations will be at the author's expense. Further details on prices are available from Cecily Pearson, Managing Editor of the Journal (613-993-9099; fax: 613-952-7656; e-mail: cecily.pearson@nrc-cnrc.gc.ca).

Preparation of electronic graphic files

General

NRC Research Press prefers the submission of electronic illustration files for accepted manuscripts and will use these electronic files whenever possible.

If electronic files are not available or if those supplied are inadequate for reproduction, hard-copy originals of adequate quality, either previously supplied or requested from the author, will be scanned. Note that the scanner will easily reproduce flaws (e.g., correction fluid, smudges). Submission of noncontinuous (screened) photographs and scanned illustrations printed out on laser printers is not recommended, as moirés develop; a moiré is a noticeable, unwanted pattern generated by rescanning or rescreening an illustration that already contains a dot pattern.

If sending hard copies, please ensure that electronic files match the hard copies (i.e., figure number and figure content). If sending a disk, on the disk label, identify (*i*) the software application and version and (*ii*) file name(s), size, and extension. If you have compressed your files, indicate what compression format was used. PC or Macintosh versions of True Type or Type 1 fonts should be used. **Do not use bitmap or nonstandard fonts.** Electronic graphics can be accepted on the following disks: 3½ in. disks, 100 MB Zip cartridge, and CD-ROM.

The preferred graphic application of NRC Research

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Press is CorelDraw! For other applications that can be used, see the electronic graphics list at http://pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_prog_e?jees_graphics_e.html.

All figures should be submitted at the desired published size. For figures with several parts (e.g., *a*, *b*, *c*, *d*, etc.) created using the same software application, assemble them into one file rather than sending several files.

Remember that the more complex your artwork becomes, the greater the possibility for problems at output time. Avoid complicated textures and shadings, especially in vector illustration programs; this increases the chance for a poor-quality final product.

Bitmap

Bitmap (raster) files are image files produced using a grid format in which each square (or pixel) is set to one level of black, colour, or grey. A bitmap (rasterized) file is broken down into the number of pixels or picture elements per inch (ppi). Pixels per inch is sometimes referred to as dots per inch (dpi). The higher the resolution of an image, the larger the number of pixels contained within the rectangular grid. The proper resolution should be used when submitting bitmap artwork. The minimum requirements for resolution are 600 dpi for line art, 1200 dpi for finelines (line art with fine lines or shading), 300 dpi for halftones and colour, and 600 dpi for combinations (halftones with lettering outside the photo area).

Colour

All colour files submitted must be as CMYK (cyan, magenta, yellow, and black). These colours are used in full-colour commercial printing. RGB graphics (red, green, and blue; colours specifically used to produce an image on a monitor) will not print correctly.

Vector

Vector files are image files produced using elements such as lines and shapes. Typically these files are used for line drawings.

Bitmap in vector

Bitmaps can be imported into vector/draw applications only for the purpose of adding and overlaying information, lines, text, etc. Bitmaps should not be resized, cropped, rotated, or otherwise manipulated after importing.

Manuscript guidelines

Style guides

As a general guide for biological terms, *The CBE Manual for Authors, Editors, and Publishers: Scientific Style and Format* (6th ed., 1994) published by the Council of Biology Editors, Inc., Chicago, IL 60603, USA, is recommended.

Spelling

Spelling should follow *Webster's Third New International Dictionary* or the *Oxford English Dictionary*. Authors are responsible for consistency in spelling.

Nomenclature, abbreviations, and acronyms

Nomenclature and abbreviations should follow the rules recommended by the International Union of Biochemistry (IUB) Committee of Editors of Biochemical Journals with support of IUPAC. As a general guide for biological terms, *The CBE Manual for Authors, Editors, and Publishers: Scientific Style Format* (6th ed., 1994), published by the Council of Biology Editors, Inc., Chicago, IL 60603, USA, is recommended. For enzyme nomenclature, *Enzyme Nomenclature (1992): Recommendations of the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology* (Academic Press, San Diego, Calif.) should be followed.

Abbreviations and acronyms that are standard in the discipline need not be defined. All others must be defined when they are first mentioned in the text and those with more than one meaning should be avoided.

Units of measurement

SI units (Système international d'unités) should be used or SI equivalents should be given. Avoid ambiguous forms such as g C/m^2/day; use g C·m^{-2}·day^{-1}. This system is explained and other useful information is given in the *Metric Practice Guide* (2000) published by CSA International (178 Rexdale Blvd., Toronto, ON M9W 1R3, Canada). For practical reasons, some exceptions to SI units are allowed. Units such as kilocalorie, reciprocal centimetre (wave number), and atmosphere may be used for the foreseeable future.

Statistical analyses

The assumptions and (or) the model underlying any statistical analysis should be clearly stated. Symbols such as * and **, denoting levels of significance, should not be used except in conjunction with the actual values of the associated test statistic; actual p values are preferred.

Fish

The Journal follows the names and spelling for fishes recommended in *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (6th ed., Spec. Publ. No. 29, American Fisheries Society, 2004) and the gene nomenclature for protein-coding loci outlined in Shaklee et al. (Trans. Am. Fish. Soc. **119**: 2–15, 1990).

Writing numbers

In writing long numbers the digits should be separated into groups of three, counted from the decimal marker to the left and right. The separator should be a space and not a comma, period, or any other mark, for example, 25 562 987 and not 25,562,987. In English text, the decimal marker should be a point, for example, 0.1 mL and not 0,1 mL. The decimal point in all numbers between 1 and –1, except 0, must be preceded by a 0. The sign × should be used to indicate multiplication, e.g., 3×10^8 and not $3 \cdot 10^8$.

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Recommandations aux auteurs

Journal canadien des sciences halieutiques et aquatiques

Orientation du Journal et directives de soumission de manuscrits

La Rédaction encourage la soumission d'articles contribuant à l'enrichissement des connaissances des sciences halieutiques et aquatiques. Les articles peuvent porter sur les cellules, les organismes, les populations, les communautés, les écosystèmes ou les procédés qui affectent les systèmes aquatiques. Ils peuvent traiter de disciplines variées y compris la biologie et l'écologie des organismes d'eau douce et d'eau salée, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, les maladies et la gestion. Les articles sont choisis selon la portée et l'importance des nouvelles connaissances ou idées qu'ils contiennent. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux.

Nous invitons les auteurs à soumettre des articles ayant des objectifs précis ou relevant des hypothèses, concepts ou questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. **La raison d'être de l'analyse et l'interprétation des résultats doivent être situées dans un vaste contexte disciplinaire ou interdisciplinaire.** Les articles de méthodologie et de modélisation doivent inclure des applications et prouver la supériorité de la méthodologie ou du modèle explicité.

La Rédaction décourage la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicable à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; ou d'articles rendant compte de l'application de normes sans gain de méthodologie. Les études préliminaires ou fragmentaires, ou dont la pertinence à grande échelle n'est pas démontrée, et les interprétations purement spéculatives sont carrément rejetées.

Les articles doivent être aussi complets que possible. S'il est impossible d'inclure toute les données pertinentes dans un seul article, l'auteur devra inclure des renvois à des articles connexes et soumettre ceux-ci avec son propre article.

Types de manuscrits

Le Journal publie le genre de textes suivants :

Articles — Études de vaste portée qui constituent de nouvelles contributions à la science.

Perspectives — Synthèses, synthèses critiques ou réévaluations de concepts ou de paradigmes couramment admis.

Discussions — Commentaire ou réplique sur des sujets récemment abordés dans le Journal.

Communications rapides — Présentations de nouveaux concepts, descriptions de nouvelles méthodologies ou courts textes sur des sujets d'actualité ou controversés.

On peut obtenir les caractéristiques précises de chacun de ces genres sur le site Web du Bureau de la rédaction (http://www.uoguelph.ca/~cjfas/).

Langue

Les manuscrits doivent être rédigés de manière claire et concise, **en français ou en anglais correct**. Les auteurs pour qui le français ou l'anglais est une langue seconde devraient faire réviser leur manuscrit par une personne dont la langue maternelle est celle du texte avant de soumettre leur manuscrit. Un style de qualité accélère et facilite l'examen et la publication des manuscrits.

Un résumé rédigé dans la langue du manuscrit doit accompagner chaque soumission. Les résumés sont traduits en anglais ou en français, selon le cas, par le traducteur du Journal. En revanche, les auteurs qui peuvent soumettre leur résumé en français et en anglais sont invités à le faire.

Frais d'impression par page

Il n'y a pas de frais d'impression par page dans le *Journal canadien des sciences halieutiques et aquatiques*.

Objectif des recommandations

Pour **faciliter la publication**, les auteurs doivent vérifier l'exactitude, l'uniformité et la lisibilité des symboles, des abréviations et des termes techniques. Les Presses scientifiques du CNRC se réservent le droit d'assurer la qualité technique du Journal. Les auteurs voudront consulter un récent numéro du Journal pour s'enquérir des exigences en matière de présentation, en particulier à l'égard des tableaux et de la bibliographie. **La non-conformité des manuscrits et des illustrations aux exigences décrites ci-dessous risque de retarder la publication.**

Soumission

Les auteurs peuvent soumettre leur manuscrit par la poste ou par le truchement du site Web.

Soumission par courrier

Nouveaux manuscrits

Les auteurs devraient soumettre par courrier **leurs manuscrits (y compris les tableaux et les illustrations) en double** à la directrice scientifique principale, *Journal canadien des sciences halieutiques et aquatiques*, Département de biologie intégrative, édifice 006, bureau 118, University of

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Guelph, Guelph, ON N1G 2W1, Canada. Veuillez inclure le texte, les tableaux et les figures du manuscrit sur disquette, en précisant le(s) progiciel(s) et la (les) version(s) utilisés; le logiciel de traitement de textes préférés est Microsoft Word pour l'**examen par les réviseurs**.

Manuscrits acceptés

Les auteurs sont priés de soumettre **une copie imprimée ainsi qu'une copie électronique (sur disquette ou cédérom ou par courriel) seulement de la version définitive du manuscrit accepté**. Si la copie électronique est présentée sur disquette ou sur cédérom, les fichiers de texte et les fichiers d'illustration doivent être soumis sur des disquettes ou cédéroms distincts. Le nom des auteurs, le nom et la version du logiciel utilisé de même que la plate-forme (IBM ou Macintosh) doivent être clairement indiqués sur chacun des supports de stockage utilisés. Le **texte** (y compris les tableaux) doit être soumis en format de traitement de texte (de préférence WordPerfect, Microsoft Word ou TeX, compatible IBM ou Macintosh). Des macros TeX pour la préparation des manuscrits sont disponibles en direct à ftp://ftp.tex.ac.uk/tex-archive/macros/latex/contrib/nrc/, ftp://ftp.dante.de/tex-archive/macros/latex/contrib/nrc/ et ftp://ctan.tug.org/tex-archive/macros/latex/contrib/nrc/. Quant aux **illustrations**, il convient de se reporter à la section « Préparation des fichiers graphiques électroniques ». Tout manuscrit devra être accompagné d'une lettre faisant foi du fait que la version du texte sur disquette reflète exactement la version imprimée définitive.

Soumission par le Web

Nouveaux manuscrits

Les auteurs peuvent soumettre leur manuscrit par le truchement d'OSPREY, le système de soumission et d'examen en direct des articles (http://pubs.nrc-cnrc.gc.ca/jcsha/osprey). OSPREY est optimisé pour les fureteurs Netscape 7.0 et Internet Explorer 6.0 (ou toute version ultérieure). Les auteurs peuvent s'inscrire sur le site à tout moment et une seule inscription est nécessaire. Au moment de l'inscription, les auteurs seront invités à choisir un nom d'utilisateur et un mot de passe. L'accès aux manuscrits est protégé par le système de nom d'utilisateur et de mot de passe.

Les auteurs qui ont besoin d'une aide technique quant au processus de soumission sur le Web peuvent communiquer avec Louis Lafleur au (613) 998-9432 ou par courriel à louis.lafleur@nrc-cnrc.gc.ca, de 8 h 00 à 16 h 00 (HNE).

Un guide de l'utilisateur détaillé est offert sur le site Web.

Les auteurs doivent accompagner leur manuscrit d'une lettre de présentation. Les tableaux et les illustrations peuvent soit faire partie du fichier de manuscrit ou être téléchargés individuellement vers le serveur. OSPREY accepte la plupart des fichiers de format texte et graphique. (Visitez le site Web pour consulter la liste complète des formats acceptés.) La soumission des manuscrits devrait se faire depuis l'ordinateur qui contient tous les fichiers pertinents. Le processus de soumission de manuscrit exige environ 10 minutes, mais le temps de téléchargement vers le serveur variera en fonction du type de connexion Internet utilisé.

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Manuscrits acceptés

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L'auteur-correspondant doit accompagner son manuscrit d'une lettre de présentation qui fait état :

(*i*) des principaux points et de l'importance du travail;
(*ii*) de la participation de tous les auteurs au manuscrit et de leur approbation de ce dernier;
(*iii*) de l'assurance que le manuscrit en question n'est pas en cours d'examen aux fins de publication dans une autre revue;
(*iv*) de suggestions quant aux arbitres éventuels;
(*v*) d'autres manuscrits, y compris de résumés détaillés, contenant une information identique ou similaire à celle contenue dans le manuscrit soumis;
(*vi*) des numéros de téléphone et de télécopieur ainsi que du courriel et de l'adresse de chaque auteur;
(*vii*) de tout conflit d'intérêts, réel ou perçu (cf. « Conflit d'intérêts et divulgation » sous la rubrique « Éthique »).

Formulaires de cession des droits d'auteur

Le manuscrit doit être accompagné de formulaires de cession des droits d'auteur dûment signés par tous les auteurs (cf. « Cession des droits d'auteur » sous la rubrique « Processus de publication »).

Emballage

L'emballage des manuscrits et des illustrations devrait être assez solide pour prévenir les dommages dus au transport.

Processus de révision

Réception des manuscrits

L'auteur-correspondant d'un manuscrit soumis, que ce dernier soit transmis par voie électronique ou par la poste, recevra, dans les plus brefs délais, un accusé de réception officiel ainsi que les formulaires à remplir et à retourner par courriel au Bureau de la Rédaction, et ce, dès que les directeurs scientifiques auront accepté d'examiner le manuscrit en vue de publication. Dans l'éventualité où un manuscrit soumis par voie électronique ne serait pas retenu pour examen en vue de publication, l'auteur-correspondant serait avisé de cette décision par courriel. S'il s'agissait d'un manuscrit soumis par courrier, le manuscrit serait retourné à l'auteur-correspondant par la poste, accompagnées d'une lettre faisant état de cette décision.

La conformité du manuscrit aux *Recommandations aux auteurs* sera vérifiée par un lecteur technique. Les manuscrits non conformes ainsi que ceux qui ne réussissent pas à définir clairement l'objet de la recherche pourront être renvoyés à l'auteur-correspondant pour que la présentation soit corrigée avant que le contenu n'en soit examiné.

Examen par les pairs/évaluation

Chaque article est habituellement soumis à une évaluation par deux réviseurs. Toutefois, la directrice scientifique principale renverra sans les évaluer tout article qui ne reflète pas la

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portée ou le caractère du Journal et les articles qui débordent des limites imposées pour la publication sous forme de « résumés approfondis ». On obtiendra les directives à cet égard sur le site Web du Bureau de la rédaction à http://www.uoguelph.ca/~cjfas/. Les articles soumis aux fins de publication dans un supplément sont soumis au même rigoureux exercice d'examen que les articles des numéros réguliers.

On demande habituellement aux auteurs d'examiner les commentaires des réviseurs et de modifier leur texte en conséquence en 90 jours, tout au plus. Faute de respecter ce délai, l'article renvoyé par l'auteur sera traité comme une nouvelle soumission à moins que l'auteur n'ait au préalable dûment communiqué avec le Bureau de la rédaction.

Manuscrits resoumis

Les auteurs qui soumettent un manuscrit précédemment refusé ou retiré doivent donner le numéro de manuscrit de leur première soumission. Les manuscrits resoumis sont traités comme de nouveaux manuscrits dans leur lettre de présentation. Les auteurs peuvent soumettre le nouveau manuscrit par courrier (avec les copies électroniques sur disquette ou cédérom), par courriel ou par le Web, accompagné d'une réponse détaillée et systématique à toutes les questions soulevées au cours de l'évaluation précédente.

Processus de publication

Généralités

La Rédaction vérifie tous les articles soumis afin de s'assurer qu'ils respectent les *Recommandations aux auteurs* et qu'ils sont accompagnés de toute la documentation d'appui nécessaire. Tout élément posant problème sera examiné par la Rédaction en consultation avec l'auteur-correspondant. Une fois que tous les problèmes sont résolus par la Rédaction et que tous les formulaires de cession des droits d'auteur dûment signés par les auteurs sont reçus, le manuscrit est acheminé aux Presses scientifiques du CNRC, à Ottawa, en vue de sa publication. La préparation finale des manuscrits est assurée par un lecteur-rédacteur responsable de l'uniformité de la présentation et du style.

Correspondance avec les Presses scientifiques du CNRC

Après qu'un article a été accepté, toute correspondance doit être adressée aux Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada (télécopieur : 613-952-7656; courriel : pubs@nrc-cnrc.gc.ca; URL : http://pubs.nrc-cnrc.gc.ca). Les Presses scientifiques du CNRC se réservent le droit d'apporter des modifications rédactionnelles mais ne modifieront pas la substance d'un article sans préalablement consulter l'auteur et la directrice scientifique principale.

Épreuves en placard

Une épreuve en placard, les épreuves d'illustration, une copie de l'article annoté et un bon de commande de tirés à part seront envoyés à l'auteur-correspondant. **Les épreuves en placard doivent être relues attentivement car elles ne seront pas revues par les Presses scientifiques du CNRC.** Elles doivent en outre être renvoyées dans les 48 heures suivant leur réception. Au stade des épreuves, il n'est plus temps d'apporter des modifications importantes ni de faire des ajouts ou des suppressions. Les frais occasionnés par des modifications excessives devront être assumés par les auteurs.

Tirés à part

Pour obtenir des tirés à part, il convient de remplir le bon de commande à cet effet, d'y annexer le paiement pertinent (chèque, numéro de carte de crédit, numéro de bon d'achat ou pièce de journal interne) et de renvoyer le tout en même temps que les épreuves et l'article corrigés. Le tarif des tirés à part commandés après la publication est fortement majoré. **Le Journal n'offre pas de tirés à part gratuits. Les tirés à part commandés ne sont postés qu'après réception d'un numéro du bon d'achat ou du paiement pertinent.**

Permission de reproduction de documents protégés par droits d'auteur

Les auteurs d'un manuscrit qui contient de la documentation déjà publiée (tableaux, illustrations, schémas, etc.), et donc assujettie aux droits d'auteur, doivent obtenir **une permission écrite, de la part du titulaire de ces droits d'auteur**, de reproduire l'information en question **en format imprimé et électronique**. Les permissions écrites doivent accompagner le manuscrit soumis, sans quoi le processus de publication pourra être retardé. Cette lettre sera exigée avec toute mention du type « Tirée de... ». Si une illustration est modifiée, de sorte qu'une telle autorisation n'est pas requise, la formulation doit être explicit : « Modifiée d'après... ». Si l'illustration est reconstituée à partir d'informations tirées d'autres auteurs la mention doit être du même type que pour une référence.

Cession des droits d'auteur

Tous les auteurs doivent remplir un formulaire de cession des droits d'auteur au CNRC. Les auteurs peuvent obtenir ces formulaires auprès du Bureau de la rédaction, dans le premier numéro d'un volume ou sur le site Web du Journal (http://pubs.nrc-cnrc.gc.ca/cgi-bin/ps/rp2_auth_f?cjfas).

Permission de republication de documentation publiée dans les revues des Presses scientifiques du CNRC

Toute demande de permission de reproduction ou de republication partielle ou intégrale d'un manuscrit doit être adressée à Roxanne Landriault, des Presses scientifiques du CNRC (613-990-2254; courriel : roxanne.landriaultn@nrc-cnrc.gc.ca).

Éthique

Généralités

Les normes d'éthique auxquelles doivent se conformer les auteurs, les examinateurs et les directeurs scientifiques sont décrites dans la Politique éditoriale des Presses scientifiques du CNRC (publiée dans le numéro de janvier 1996 du *Journal canadien des sciences halieutiques et aquatiques*, diffusée sur le site Web du Journal à http://pubs.nrc-cnrc.gc.ca/cgi-bin/ps/rp2_cust_f?pubpolicy ou disponible auprès des Presses scientifiques du CNRC).

Reproduction et rediffusion

En vertu d'une politique de longue date, le *Journal canadien des sciences halieutiques et aquatiques* refuse de publier des articles qui ont été publiés ailleurs. La directrice scientifique principale juge un manuscrit inadmissible si le

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manuscrit en question (*i*) est en cours d'examen en vue d'être publié ou a déjà été publié dans un périodique ou dans un livre, (*ii*) est en cours d'examen en vue d'être publié ou a déjà été publié dans un compte rendu de conférence ou dans une publication officielle ouvertement distribuée à plus de 100 exemplaires. Les auteurs peuvent proposer, sur leur site Web ou sur le serveur de leur institution, une ébauche d'un article soumis, à condition que l'ébauche ne soit aucunement modifiée après l'acceptation du manuscrit. Les auteurs sont invités à inclure, sur la version préimprimée de leur manuscrit, un lien hypertexte vers sa version définitive sur le site Web des Presses scientifiques du CNRC (http://pubs.nrc-cnrc.gc.ca). Les résumés concis ou détaillés inclus dans les comptes rendus de conférences ne constituent pas une « publication antérieure ». Un « résumé détaillé » est un document de 1000 mots ou moins qui ne comprend ni tableaux détaillés ni illustrations des résultats de l'étude. Des renseignements supplémentaires sur les résumés détaillés sont disponibles sur le site Web du Bureau de la rédaction (http://www.uoguelph.ca/~cjfas/).

Déclaration de la paternité du manuscrit

Dans sa lettre de présentation, l'auteur-correspondant doit garantir que les auteurs ont tous contribué de près au manuscrit et ont approuvé la version soumise.

Suggestion d'examinateurs

Les auteurs peuvent suggérer des examinateurs. Ils doivent fournir l'adresse complète, les numéros de téléphone et de télécopieur, ainsi que l'adresse de courriel (dans la mesure du possible) de ces personnes. Les directeurs scientifiques ne sont aucunement tenus de se limiter à ces suggestions.

Conflit d'intérêts et divulgation

La directrice scientifique principale reconnaît la possibilité que des conflits d'intérêts réels ou perçus surviennent à la suite de circonstances intellectuelles, personnelles ou financières liées aux travaux de recherche. Les manuscrits doivent inclure une divulgation de toute source de financement de la recherche. De plus, la lettre de présentation doit expliquer tout conflit d'intérêts, réel ou perçu, qui pourrait survenir lors du processus d'examen par les pairs. Si de tels conflits ne sont pas divulgués, le manuscrit pourrait être refusé.

Retouche photographique

Le Journal estime que les photographies numériques font partie des données. Aussi est-il impératif que les images numériques soumises reproduisent fidèlement l'image d'origine. Toute retouche à l'aide d'un logiciel graphique doit être explicitée dans les méthodes, notamment quant au logiciel utilisé et aux techniques appliquées pour améliorer ou modifier l'illustration. Une telle explication assure la constance des méthodes et l'intégrité scientifique des travaux. La suppression des artéfacts ou de toute donnée non essentielle contenue dans l'image est découragée.

Sections du manuscrit

Disposition et organisation

Le manuscrit doit être composé à **double interligne**, d'un seul côté de feuilles de 21,5 sur 28 cm (8,5 po sur 11 po ou ISO A4). Chaque page doit être numérotée, en commençant par la page de titre. Le texte destiné à être publié en italique doit être présenté en italique, non pas souligné. Les auteurs utiliseront des caractères en majuscule seulement lorsque cela s'avèrera pertinent.

Les auteurs devraient structurer le manuscrit en fonction de l'énoncé des objectifs ou de la portée de l'étude présentée dans l'introduction. Il est particulièrement important que le titre et les en-têtes reflètent l'énoncé des objectifs.

Avant de commencer la rédaction du manuscrit, les auteurs devraient dresser une liste provisoire des en-têtes, avec le moins de subdivisions possible, et remanier cette liste jusqu'à ce qu'elle reflète une démarche logique, intelligible pour le lecteur. Habituellement, l'ordre chronologique ne sera pas satisfaisant. En effet, il sera plus facile de suivre le texte si les méthodes, les résultats et la discussion font partie de sections distinctes.

Les auteurs devraient organiser les tableaux et les illustrations de manière à faciliter les comparaisons et regrouper les données apparentées de façon à réduire au minimum le nombre de tableaux et d'illustrations. Dans la mesure du possible, les tableaux et les figures devraient être suffisamment explicites pour que le lecteur n'ait pas à se reporter au texte.

Les auteurs devraient commencer les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés pointus. La présentation de la conclusion dans un premier temps et de sa justification dans un deuxième facilite considérablement la lecture et l'évaluation par les scientifiques. Lors de la rédaction des manuscrits, le défaut le plus courant consiste à omettre de présenter dès le début du texte les généralités les plus dignes de mention.

Les auteurs doivent veiller à ce que le contenu de chaque section soit pertinent à l'en-tête et que le contenu de chaque paragraphe se rapporte à la première phrase du paragraphe (la « phrase d'ouverture »).

Avant de rédiger les paragraphes, les auteurs devraient composer la phrase d'ouverture de chaque paragraphe et disposer chacune de celles-ci dans l'ordre approprié.

Titre

Les auteurs doivent limiter le titre à ce que démontre le manuscrit. Le titre est un élément fondamental de l'article et doit refléter clairement et brièvement le contenu du manuscrit. Le titre a deux fonctions : (*i*) il permet au lecteur de juger si, oui ou non, l'article est susceptible de l'intéresser et (*ii*) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance potentielle du contenu. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, le cas échéant, la démarche technique (p. ex. radiographie, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à... » ou « Recherche sur... ». Des titres judicieux facilitent considérablement le classement des publications et leur utilisation par les scientifiques et les bibliothécaires et de même que leur dépouillement par les indexateurs. Les titres en série devraient être évités.

Page de titre

La page de titre doit comprendre les suivants. (*i*) Le titre intégral du manuscrit. (*ii*) Le nom des auteurs, dans l'ordre dans lequel ces noms doivent apparaître dans l'intitulé de l'article imprimé. (*iii*) L'affiliation et l'adresse (y compris l'adresse de courriel) de chaque auteur pendant les recherches. Les changements d'affiliations et d'adresses (y compris d'adresse de courriel) devront être indiqués en note infrapagi-

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nale. (*iv*) Le nom, l'adresse, les numéros de téléphone et de télécopieur ainsi que l'adresse de courriel de l'auteur-correspondant.

Nom des auteurs

La directrice scientifique principale encourage tous les auteurs à fournir leur prénom au complet plutôt qu'une simple initiale.

Résumé

Chaque contribution doit être accompagnée d'un résumé qui utilisera un vocabulaire évocateur, susceptible de capter l'intérêt des lecteurs visés. Ceci est particulièrement important en vue du dépouillement automatisé que font les services de repérage de l'information de même que les robots des moteurs de recherche. Un résumé comptera au plus 175 mots et sera présenté sur une page distincte. Le résumé concis doit refléter précisément le contenu du manuscrit et doit compléter le titre plutôt que simplement le reprendre. Les résumés sont traduits en anglais ou en français, selon le cas, par les traducteurs du Journal. En revanche, les auteurs qui peuvent soumettre leur résumé en français et en anglais sont invités à le faire. Le résumé ne devrait pas contenir de références à moins que cela ne soit essentiel. Dans ce dernier cas, il faudra fournir l'information bibliographique intégrale.

À l'instar du titre, le résumé permet au lecteur de prendre connaissance du contenu du manuscrit et de décider si, oui ou non, il lui faut le lire en entier. Les auteurs devraient présenter, au début du résumé, la principale conclusion de l'étude et l'appuyer par les résultats pertinents. Ils ne doivent donner que les détails des méthodes nécessaires à la compréhension de la démarche et les intégrer à l'énoncé des résultats. Il faut éviter l'emploi de phrases telles que « … on y analyse » ou « … a été trouvé » et être plus spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et les indexateurs et qu'il s'agit parfois de la seule partie de l'article que certains lecteurs auront l'occasion de voir, il importe qu'il reflète précisément le contenu du manuscrit et qu'il soit complet en lui-même, c.-à-d. qu'il contienne seulement des références absolument essentielles et facilement retraçables (p. ex. R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. 37 : 268–282).

Introduction

Les auteurs doivent limiter l'introduction à la portée, au but et à la raison de l'étude. Ils ne mentionneront que les travaux publiés et autres documents nécessaires à la définition du problème et du contexte. Les auteurs devraient tout d'abord décrire le but ou la portée de l'étude, définir ensuite le problème puis présenter des repères qui orienteront le lecteur. En général, une introduction comprendra de 375 à 500 mots.

Matériel et méthodes

La section « Matériel et méthodes » jette les fondations de la résolution du problème posé dans l'énoncé du travail.

Les auteurs limiteront les renseignements sur le matériel et les méthodes à ce qui est nécessaire pour juger de la validité des résultats. Cette évaluation sera facilitée si toute l'information connexe est présentée, autant que possible, dans une même section. S'il s'agit d'outillage ou de techniques connus, les auteurs incluront des références aux publications et ne décriront en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : « Afin de déterminer… nous… ». Si la section est longue, les auteurs devraient la diviser à l'aide d'en-têtes correspondant aux en-têtes de la section des résultats.

Résultats

Les auteurs doivent limiter les résultats aux réponses apportées aux questions en rapport avec l'énoncé de travail et faire en sorte que ces réponses soient aussi complètes que possible tout en étant concises. Les résultats doivent être associés aussi étroitement que possible aux observations ou aux mesures, ceci afin que le lecteur ne confonde pas constatations et spéculations. Les auteurs devraient dégager les principales constatations mises en évidence par les tableaux et les illustrations et éviter de répéter dans le texte ce que les légendes expriment clairement. La documentation complémentaire au texte peut faire partie de la documentation du rapport intégral ou être versée dans un dépôt de données reconnu. Les auteurs peuvent y faire référence dans le texte (cf. section « Données supplémentaires »).

Discussion

Les auteurs devraient limiter la discussion à la présentation des principales contributions de l'étude et à l'interprétation de constatations particulières, en les comparant avec celles d'autres auteurs. Ils mettront l'accent sur la synthèse, l'interprétation et la présentation de généralisations et de principes largement applicables. S'il existe des exceptions ou des aspects douteux, les auteurs le souligneront et feront ressortir la manière dont les résultats corroborent ou contredisent les travaux déjà publiés. La spéculation doit se limiter à ce qui peut être appuyé sur des preuves raisonnables. Les auteurs devraient terminer cette section par un sommaire de l'importance du travail et par les conclusions qu'il a invitées. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule section.

Remerciements

Les remerciements sont rédigés à la troisième personne. Les auteurs sont priés de limiter les remerciements aux personnes qui ont étroitement contribué aux aspects scientifiques et techniques de l'article, qui ont fourni une aide financière ou qui ont sensiblement amélioré la qualité de la présentation. Les remerciements ne devraient pas viser les fournisseurs de service de soutien.

Notes infrapaginales

Les notes infrapaginales ne devraient figurer dans le corps du texte que lorsqu'elles sont indispensables; toutefois, leur utilisation dans les tableaux est encouragée. Lorsque des notes infrapaginales figurent dans le texte, les appels devraient être signalés à l'aide d'un chiffre arabe en exposant (sauf dans le cas des tableaux, cf. ci-dessous) et numérotés de façon consécutive à partir de la première note infrapaginale, y compris toute note apparaissant en page titre. Chaque note infrapaginale doit figurer au bas de la page où elle est signalée, pas dans la bibliographie.

Équations et liste de symboles

Les **équations** doivent être clairement dactylographiées et, si elles incluent des exposants ou des indices, être dactylographiées à triple interligne. Les exposants et les indices doivent être lisibles et correctement placés. Il convient de rendre évidente la distinction entre la lettre *l* et le chiffre *un*, et entre

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la lettre majuscule *O* et le chiffre *zéro*. Une lettre ou un symbole ne devrait être associé qu'à une seule réalité et devrait être utilisé de façon uniforme dans l'article. Chaque variable doit être définie dans le texte ou dans une **liste des symboles** qui succédera à la bibliographie. Les variables représentant des vecteurs, des matrices, des matrices vectorielles et des tenseurs doivent être clairement définies. Les équations doivent être identifiées à l'aide de chiffres arabes placés entre parenthèses, alignés avec la **marge de gauche**. Aucune distinction n'est faite entre la numérotation des formules mathématiques et celle des formules chimiques.

Références

Présentation générale

Il appartient aux auteurs d'assurer l'adéquation entre le contenu des références bibliographiques et l'information bibliographique des publications citées. Dans le texte, les références doivent être signalées à l'aide du nom des auteurs et de l'année de publication, p. ex. (Martial 1970) ou Dupont et Tremblay (1990), selon la structure de la phrase. Lorsqu'il y a trois auteurs ou plus, le nom du premier auteur est suivi de la mention et *al.* (p. ex. Dupont et *al.* 1991). Lorsque le nom et l'année ne suffisent pas à distinguer deux ouvrages, les lettres *a*, *b*, *c*, etc. sont ajoutées après l'année (à la fois dans le texte et dans la bibliographie), p. ex. Dupont 1983*a*, 1983*b*; Dupont et al. 1980*a*, 1980*b*).

Les adresses Web (adresses URL) ou les identificateurs d'objets numériques (système DOI) permettent de consulter les références qui sont accessibles sur le Web. Les auteurs sont invités à les utiliser et à les inclure avec les références dans la bibliographie (voir exemple ci-dessous).

Rapports non publiés, communications personnelles et documents sous presse

Les références bibliographiques à des rapports non publiés, à des communications personnelles ou à des articles en cours d'examen ne paraîtront pas dans la bibliographie. Elles seront plutôt signalées sous forme de notes infrapaginales ou entre parenthèses dans le texte. Elles devront contenir le nom des auteurs et leur initiale. Dans le cas des communications personnelles, il convient de préciser la nature de la source et l'année (p. ex. J.S. Ernst (communication personnelle, 1999)). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. Si un livre ou un article non publié avéré est **en attente de publication**, sa référence doit apparaître dans la bibliographie et porter la mention « sous presse ». Dans ce cas, il ne faut pas préciser le volume et le numéro de la page, puisque cette information risque de changer lors du processus de publication.

Présentation de la bibliographie

Dans la **bibliographie**, qui apparaît à la suite du texte, les références sont composées à double interligne et classées par ordre alphabétique du nom du premier auteur, sans numérotation. Si la bibliographie comprend plusieurs publications d'un même premier auteur, les règles suivantes s'appliquent : (*i*) les articles avec **un seul auteur** sont signalés en premier, par ordre chronologique, en commençant par le plus ancien; (*ii*) viennent ensuite les articles avec **deux auteurs**, en ordre alphabétique du nom de famille du second auteur; (*iii*) puis viennent les articles de **trois auteurs et plus**, en ordre chronologique.

Directives générales quant aux références

On choisira les références avec soin, les limitant aux publications importantes. Les références doivent refléter le style des numéros récents du Journal. Le titre d'une revue doit être abrégé conformément au *Chemical Abstracts Service Source Index* (*CASSI*) (Chemical Abstracts Service, 2540 Olentangy River Road, P.O. Box 3012, Columbus, OH 43210-0012, É.-U.) ou à *BIOSIS Serial Sources* (BIOSIS, 2100 Arch Street, Philadelphia, PA 19103-1399, É.-U.). En cas de doute, les auteurs doivent écrire le nom de la revue au complet. Nous recommandons aux auteurs de préciser le numéro des revues citées et de l'indiquer entre parenthèses après le numéro du volume. La liste de références qui suit reflète les normes de ponctuation, de présentation et d'abréviation préconisées.

Exemples de divers types de références, y compris les références à des documents électroniques

Article de revue comprenant un système DOI :

Newbury, M.G., et Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. doi:10.1139/F04-113.

Article de revue comprenant une adresse Web :

Newbury, M.G., et Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. Disponible à http://pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_f?cjfas_f04-113_61_ns_nf [cité 28 October 2005].

Article de revue disponible en ligne seulement (identificateur DOI) :

van der Sanden, J.J., et Hoekman, D.H. 2005. Review of relationships between grey-tone co-occurrence, semivariance, and autocorrelation based image texture analysis approaches [en ligne]. Can. J. Remote Sens. **31**(3): 207–213. doi:10.1139/rs03-011.

Numéro intégral d'une revue :

Gordon, D.C., Jr., et Hourston, A.S. (*directeurs de la rédaction*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40** (Suppl. 1).

Rapport :

Pigeon, M., et Langlois, M. 1987. Étude de la durabilité au gel d'un ciment avec fumée de silice. Ciments Saint-Laurent, Beauport (Québec). Rapp. GCT-87-09.

Livre :

Lacroix, P., et Lalonde, J. (*directeurs de la rédaction*).1992. Les grands barrages. Éditions Poly-Sciences, Montréal (Québec).

Livre faisant partie d'une collection :

Scott, W.B., et Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. n° 184.

Section d'un livre :

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, Britsh Columbia. *Dans* Salmonid ecosystems of the North Pacific. *Sous la direction de* W.J. McNeil et D.C. Himsworth. Oregon State University Press, Corvallis (Oregon). p. 203-229.

Article d'un compte rendu de conférence :

Milot. D. 1973. Le barrage de Montreuil. *Dans* Les grands barrages. *Sous la direction de* F. Wang et C. Dulude. 2e Symposium international sur les barrages, Chicoutimi

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(Québec), 8 au 10 mai 1972. Éditions P. Lacoste, Montréal (Québec). p. 102-150.

Publication ou brochure d'institution :

Dzikowski, P.A., Kirby, G., Read, G., et Richards, W.G. 1984. The climate for agriculture in Atlantic Canada. Disponible auprès du Atlantic Advisory Committee on Agrometeorology, Halifax (Nouvelle-Écosse). Publ. ACA 84-2-500. N° Agdex 070.

Auteur collectif :

American Public Health Association, American Water Works Association et Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14e éd. American Public Health Association, American Water Works Association et Water Pollution Control Federation, Washington (District de Columbia).

Mémoire :

Keller, C.P. 1987. The role of polysaccharidases in acid wall loosening of epidermal tissue from young *Phaseolus vulgaris* L. hypocotyls. Mémoire de maîtrise ès sciences, Département de botanique, The University of British Columbia, Vancouver (Colombie-Britannique).

Document sur un site Web :

Quinion, M.B. 1998. Citing online sources: advice on online citation formats [en ligne]. Disponible à http://www.worldwidewords.org/articles/citation.htm [cité le 20 octobre 2005].

Traduction :

Koike, A., et Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1-11. [Traduit du japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983.]

Tableaux

Les tableaux, qui occuperont chacun une page distincte, doivent suivre la bibliographie, être numérotés de façon continue en chiffres arabes dans l'ordre de mention dans le manuscrit et comporter un bref titre descriptif, d'au plus une phrase, intelligible sans qu'il ne soit nécessaire de se reporter au texte. Les titres de colonne doivent être brefs, mais peuvent être étoffés à l'aide de notes infratabulaires. Les tableaux ne doivent pas contenir de traits verticaux. Les auteurs voudront consulter un exemplaire du Journal pour s'enquérir de la présentation souhaitable des tableaux. Les notes infratabulaires doivent être signalées par des symboles (selon l'ordre suivant : *, †, ‡, §, ||, ¶, #) ou des lettres minuscules en italique placées en exposant. Une note descriptive qui n'est pas introduite par un appel de note peut être inscrite au bas du tableau à titre de **Nota**. Les auteurs éviteront d'insérer de nombreux petits tableaux et garderont le nombre de tableaux au minimum.

Légendes des illustrations

Les légendes des illustrations doivent constituer une liste **sur une page distincte**, qui suivra les tableaux. Les légendes devraient être descriptives de sorte qu'il ne soit pas nécessaire de se reporter au texte. Elles ne devraient pas inclure d'information expérimentale : celle-ci aura plutôt été présentée comme il se doit dans la section « Méthodes ». Dans les graphiques, les légendes ne doivent pas reprendre le label des axes mais plutôt décrire ce que révèlent les données. Dans le cas de montages d'illustrations, les auteurs rédigeront une légende globale contenant suffisamment d'information pour décrire l'ensemble du montage. Si chaque élément mérite sa propre légende, le montage sera fractionné et les illustrations seront plutôt présentées de façon individuelle.

Annexes

Une annexe est un document distinct et complet. Les illustrations et les tableaux présentés dans les annexes doivent être numérotés de façon consécutive, distinctement des illustrations et tableaux du corps de l'article, p. ex. figure A1, tableau A1, etc. Si les annexes contiennent des références bibliographiques, ces dernières doivent apparaître dans une bibliographie distincte de la biographie du corps de l'article. S'il y a plus qu'une annexe, veuillez les identifier de la façon suivante : Annexe A, Annexe B, etc.

Données supplémentaires

Les données supplémentaires comprennent des tableaux, des figures (cartes), des calculs détaillés et des ensembles de données produits par les auteurs dans le cadre de leur recherche, mais qui ne sont pas essentiels à la compréhension ni à l'évaluation de l'article, et qui ne seront pas publiés dans la version imprimée du Journal. Selon la politique du Journal, les données de ce genre peuvent ou non être évaluées par les pairs. Les données supplémentaires doivent être soumises avec l'article. Pour la soumission en direct (OSPREY), joindre les fichiers concernés à la rubrique « Données supplémentaires ». Pour les envois postaux, indiquer clairement quelles sont les données supplémentaires. Le Conseil national de recherches du Canada administre un dépôt des données non publiées dans lequel les données supplémentaires peuvent être versées, à la demande des auteurs ou de la directrice scientifique principale. De plus, il maintenant est possible d'accéder à ces données dans leur format d'origine à partir du site Web du Journal, grâce aux hyperliens à cet effet apparaissant sur la version Web de l'article. Les tableaux et les illustrations doivent être numérotés de façon consécutive, distinctement de ceux destinés à la publication (p. ex. figure S1, tableau S1). Chaque ensemble de données supplémentaires doit faire l'objet d'une note infrapaginale dans l'article imprimé. Des exemplaires des données déposées peuvent être obtenus contre paiement auprès du Dépôt des données non publiées, ICIST, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada.

Programmes informatiques

La Rédaction ne publie habituellement pas les imprimés détaillés produits à l'aide de programmes informatiques. Si les données contenues dans un tel imprimé contribuent sensiblement à la valeur de l'article, l'auteur doit mettre deux copies du programme en dépôt (cf. section « Données supplémentaires »).

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Les auteurs doivent soumettre les illustrations originales et deux copies des illustrations au Bureau de la rédaction, même si seul le fichier électronique est destiné à servir à la publication.

Chaque illustration ou groupe d'illustrations doit être préparé de manière à occuper, après réduction, l'espace d'une ou deux colonnes du texte. Les dimensions définitives maximales d'une illustration sur une colonne sont de 8,6 sur 23,7 cm (3,4 sur 9,3 po) et celles d'une illustration sur deux colonnes de 18,2 sur 23,7 cm (7,2 sur 9,3 po). Les illustrations (y compris les similis) sont numérotées en chiffres arabes de façon consécutive. Elles doivent toutes être signalées dans l'article et être intelligibles sans qu'il ne soit nécessaire de se reporter au texte. Tous les termes, les abréviations et les symboles qu'elles contiennent doivent être identiques à

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L'épaisseur des traits doit être suffisante (au moins 0,5 point) pour que la reproduction soit nette; tous les symboles, les exposants, les indices et les signes décimaux doivent être proportionnés au reste du dessin et d'une dimension suffisante pour permettre la réduction nécessaire sans perte de détail. Il convient de ne pas utiliser de petits symboles ouverts, qui ont tendance à se refermer lorsqu'ils sont reproduits. **Les caractères d'imprimante à points, de machine à écrire ou écrits à la main ne sont pas acceptables.** Les illustrations de dimensions semblables doivent afficher le même style de police et la même dimension de caractère. Les imprimés originaux des **spectromètres RMN, IR, RPE,** etc. ne sont pas acceptables. Ils doivent être retracés au propre. Les **dessins au trait originaux soumis sur papier** doivent être faits à l'encre noire ou produits par ordinateur à l'encre noire sur du papier blanc de première qualité ou sur un support comparable. Quant aux dessins produits par ordinateur, il convient de fournir un imprimé au laser de la meilleure résolution disponible.

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Les cartes doivent avoir des **motifs clairs et gras**, et comporter les longitudes et latitudes (ou les coordonnées de Mercator transverses universelles) de même qu'une échelle graphique, ceci afin de pouvoir repérer avec exactitude l'emplacement du travail. Sur **les cartes du Québec**, le nom officiel des municipalités doit être utilisé (p. ex. Québec, Montréal, Clarke City). De plus, le nom des éléments topographiques doit systématiquement être en français (p. ex. Lac Bienville), à l'exception des noms d'intérêt pancanadien. En effet, ces noms ont une version officielle française et anglaise (p. ex. « Océan Atlantique » et « Atlantic Ocean ») et doivent donc être présentés dans la langue de l'article. La province de Québec, dans les cartes en anglais, doit être désignée « Quebec ». Les auteurs trouveront une liste complète des noms des régions d'intérêt pancanadien dans *Le guide du rédacteur* (p. 236-237, 2e édition, 1996), publié par Travaux publics et Services gouvernementaux Canada, Ottawa, ON K1A 0S5.

Photographies

Les photographies doivent être en ton continu, de première qualité, avec contrastes bien marqués, rognées de façon à ne laisser paraître que les éléments essentiels. Une photographie ou un groupe de photographies doit être préparé de manière à occuper, **sans réduction supplémentaire**, une ou deux colonnes du texte. Les micrographies électroniques et les photomicrographies doivent comporter une échelle graphique à même le cliché. Pour assurer un bon résultat de la reproduction, les auteurs uniformiseront le contraste et la densité de toutes les photographies montées sur une même planche. Les **photographies soumises sur papier** doivent être imprimées sur papier glacé. Elles doivent être rognées et montées sur carton bristol blanc **mince**. Les photographies en montage doivent être juxtaposées sans espace.

Illustrations en couleur

Les illustrations en couleur sont reproduites aux frais de l'auteur. Les auteurs qui désirent en savoir davantage doivent communiquer avec la rédactrice administrative du Journal, Cecily Pearson (613-993-9099; télécopieur : 613-952-7656; courriel : cecily.pearson@nrc-cnrc.gc.ca).

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Le logiciel graphique que préconisent les Presses scientifiques du CNRC est CorelDraw! Pour connaître les applications compatibles, les auteurs peuvent se reporter à la liste des programmes graphiques électroniques à http://pubs.nrc-cnrc.gc.ca/cgi-bin/ps/rp2_prog_f?jees_graphics_f.html.

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Il convient de garder les illustrations le plus simple possible afin d'éviter les complications. Les auteurs voudront éviter les textures et les fonds grisés compliqués, particulièrement dans les programmes d'illustration vectorielle, puisque ceci risque d'altérer la qualité des illustrations au moment du tirage.

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suivantes : 600 ppp pour les dessins au trait, 1200 ppp pour les traits fins (les dessins au trait comportant des traits fins ou un fond grisé), 300 ppp pour les similis et les couleurs et 600 ppp pour les combinaisons (similis avec caractères à l'extérieur de l'espace réservé à la photo).

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Directives pour les manuscrits

Guides de style

Il est recommandé d'utiliser, comme guide général dans le domaine de la biologie, *The CBE Manual for Authors, Editors, and Publishers : Scientific Style and Format* (6e édition, 1994), publié par le Council of Biology Editors, Inc. (Chicago, IL 60603, É.-U.).

Orthographe

L'orthographe doit respecter celle du *Petit Robert*. Les auteurs sont responsables de l'uniformité de l'orthographe dans l'ensemble du texte. Les accents doivent être insérés sur les majuscules.

Nomenclature, abréviations et acronymes

La nomenclature et les abréviations doivent être conformes aux règles proposées par la Commission des rédacteurs de revues de biochimie de l'Union internationale de biochimie (UIB) en collaboration avec l'UICPA. Il est recommandé d'utiliser, comme guide général dans le domaine de la biologie, *The CBE Manual for Authors, Editors, and Publishers : Scientific Style and Format* (6e édition, 1994), publié par le Council of Biology Editors, Inc. (Chicago, IL 60603, É.-U.). En matière de nomenclature des enzymes, il convient de consulter la publication *Enzymes nomenclature (1992): Recommendations of the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology* (Academic Press, San Diego (Californie)).

Il n'est pas nécessaire de définir les abréviations et les acronymes d'usage courant dans le domaine. Toutes les autres doivent être définis à la première mention dans le texte et ceux ayant plus d'une signification ne devraient pas être utilisés.

Unités de mesure

Il est recommandé de se servir du **Système international d'unités** ou, à tout le moins, de fournir les équivalences en unités SI. Éviter les formes ambiguës, telles que g C/m^2/jour; utiliser plutôt g $C \cdot m^{-2} \cdot jour^{-1}$. Ce système est décrit dans le *Guide de familiarisation au système métrique*, CAN/CSA-Z234.1-00, publié par l'Association canadienne de normalisation (178, boulevard Rexdale, Toronto, ON M9W 1R3, Canada). Pour des raisons pratiques, la Rédaction admet parfois certaines exceptions à l'utilisation du Système international d'unités.

Analyses statistiques

Les hypothèses ou le modèle sous-jacent à toute analyse statistique doit être clairement énoncé. Les symboles * et **, indiquant les niveaux de signification, ne doivent être utilisés que s'ils sont accompagnés des valeurs réelles de la valeur à tester. Il est préférable d'utiliser les valeurs réelles de *p*.

Poissons

Pour le nom des poissons et leur orthographe, le Journal adhère aux recommandations contenues dans *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (6e éd., Spec. Publ. No. 29, American Fisheries Society, 2004). Pour la nomenclature génétique pour les loci de codage des protéines, le Journal adhère aux recommandations contenues dans Shaklee et al. (Trans. Am. Fish. Soc. **119** : 2–15, 1990).

Nombres

Les nombres de cinq chiffres ou plus sont répartis en groupes de trois à partir du signe décimal, à gauche comme à droite, puis séparés par un espace (pas un point, ni une virgule ou autre symbole); on aura ainsi 23<I>562<I>987 et non pas 23,562,987. En français, le signe décimal est la virgule (p. ex. 0,1 mL) et il est précédé d'un zéro pour les nombres entre 1 et -1, sauf pour le zéro. Le symbole × indique la multiplication (p. ex. 3×10^6 et non pas $3 \cdot 10^6$).

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13.(3) *Lorsque l'auteur est employé par une autre personne en vertu d'un contrat de louage de service ou d'apprentissage, et que l'oeuvre est exécutée dans l'exercice de cet emploi, l'employeur est, à moins de stipulation contraire, le premier titulaire du droit d'auteur; mais lorsque l'oeuvre est un article ou un autre contribution, à un journal, à une revue ou à un périodique du même genre, l'auteur, en l'absence de convention contraire, est réputé posséder le droit d'interdire la publication de cette oeuvre ailleurs que dans un journal, une revue ou un périodique semblable.*

La seule exception dans la cession du droit d'auteur est lorsque le document est associé au droit d'auteur de la Couronne, qui appartient au gouvernement du Canada .

12. *Sous réserve de tous les droits ou privilèges de la Couronne, le droit d'auteur sur les oeuvres préparées ou publiées par l'entremise, sous la direction ou la surveillance de Sa Majesté ou d'un ministère du gouvernement, appartient, sauf stipulation conclue avec l'auteur, à Sa Majesté et, dans ce cas, il subsiste jusqu'à la fin de la cinquantième année suivant celle de la première publication de l'oeuvre.*

Les gouvernements, en particulier le gouvernement fédéral, ne disposent pas d'un mécanisme simple de cession de droit d'auteur pour ce genre de biens de la Couronne. C'est pourquoi lorsqu'un auteur est un fonctionnaire et que, par conséquent, le droit d'auteur appartient à la Couronne, une simple permission d'usage est suffisante pour l'éditeur, pour autant que celle-ci ait été octroyée par une personne jouissant de l'autorité nécessaire pour ce faire.

ANNOUNCEMENT

Call for nominations for prestigious Canadian Ocean Sciences Medal

It is time to send in nominations for the next Timothy R. Parsons Medal, Canada's prestigious new award for distinguished accomplishments in multidisciplinary facets of ocean sciences. The Department of Fisheries and Oceans (DFO) established the award in 2004 and the next award will be presented at the Canadian Meteorological and Oceanographic Society (CMOS) Congress in May 2006 in Toronto.

Eligible scientists are those working for Canadian institutions for the benefit of Canadian science, and the nomination can be for a lifetime's body of work or for a recent outstanding achievement. To facilitate nominations, an online nomination form has been created, at http://www.dfo-mpo.gc.ca/science/Awards/Persons_e.htm.

The award is named for Dr. Tim Parsons, Professor Emeritus at the University of British Columbia and an Honorary Research Scientist at the Institute of Ocean Sciences in Sidney, B.C. His lifetime work established a new ecosystem approach for the management of fisheries using oceanographic information. Previous recipients included Dr. Parsons himself, and Dr. Daniel M. Ware, for his outstanding contribution to the field of fisheries oceanography.

How to nominate a scientist for the Timothy R. Parsons Medal

The deadline for nominations is February 28, 2006. Any Canadian may nominate a potential recipient. The award is granted annually, contingent on the selection committee finding a worthy recipient, and nominees from the previous year are automatically reconsidered. Letters of support from co-nominators are welcome, but not necessary. Each nomination should be supported by a concise, comprehensive statement indicating the merits and contributions made by the nominee to multidisciplinary ocean science. The statement should be supported by references to significant ideas, publications, teaching activities, and program leadership. The supporting information should include a summary of the accomplishments of the individual and a statement indicating how these accomplishments were connected with the progress of multidisciplinary ocean science.

Please use the on-line form at http://www.dfo-mpo.gc.ca/science/Awards/Persons_e.htm or send nominations to:

Timothy R. Parsons Medal Committee
Strategic Science Outreach
Stn. 8W144 – 200 Kent Street
Ottawa, Ontario, K1A 0E6
Tel: (613) 991-1021
FAX: (613) 990-5113
ssopss@dfo-mpo.gc.ca

COMMUNIQUÉ

Appel de candidatures pour la prestigieuse médaille dans le domaine des sciences de la mer au Canada

Il est maintenant temps de soumettre les candidatures pour la prochaine remise de la médaille Timothy R. Parsons, le nouveau prestigieux prix du Canada décerné aux scientifiques s'étant distingués dans un domaine multidisciplinaire lié aux sciences de la mer. Ce prix a été créé par le ministère des Pêches et des Océans (MPO) en 2004 et la prochaine médaille sera remise lors du congrès de la Société canadienne de météorologie et d'océanographie (SCMO) à Toronto en mai 2006.

Les scientifiques qui sont admissibles doivent oeuvrer au sein d'une institution canadienne dans l'intérêt de la science. Les candidatures peuvent avoir pour but de faire reconnaître l'ensemble d'une carrière ou une réalisation exceptionnelle récente. Dans le but de faciliter le processus de mise en candidature, un formulaire en ligne a été créé à l'adresse suivante : http://www.dfo-mpo.gc.ca/science/awards/persons_f.htm

La médaille a été nommée en l'honneur de M. Tim Parsons, professeur émérite à l'Université de la Colombie-Britannique et chercheur honoraire à l'Institut des sciences de la mer de Sidney, en Colombie-Britannique. Au cours de sa carrière, il a mis au point une nouvelle approche écosystémique intégrant des données océanographiques pour la gestion des pêches. Les précédents récipiendaires de la médaille sont M. Parsons lui-même ainsi que M. Daniel M. Ware qui s'est mérité la médaille pour sa remarquable contribution à l'océanographie des pêches.

Mise en candidature d'un scientifique pour la médaille Timothy R. Parsons

La date limite pour les mises en candidatures est le 28 février 2006. Tout Canadien peut proposer un candidat potentiel. La médaille est remise chaque année à condition que le comité de sélection ait identifié un récipiendaire méritoire. Les candidatures de l'année précédente sont automatiquement réexaminées. Les lettres d'appui de la part de collègues seront acceptées, mais elles ne sont pas nécessaires. Il importe que chaque mise en candidature soit appuyée par une déclaration concise et exhaustive indiquant le bien-fondé de la contribution apportée par la personne proposée aux sciences multidisciplinaires de la mer. La déclaration doit faire référence à des activités d'enseignement, à des idées importantes, à des activités démontrant le leadership et une liste de publications. L'information d'appui doit comprendre le résumé des réalisations de la personne et une déclaration montrant comment ses réalisations ont contribué à l'avancement des sciences multidisciplinaires de la mer.

Veuillez utiliser le formulaire en ligne à : http://www.dfo-mpo.gc.ca/science/awards/persons_f.htm ou faites parvenir les candidatures à l'adresse suivante :

Comité de la médaille Timothy R. Parsons
Bureau de la promotion stratégique des sciences
200, rue Kent, bureau 8W144
Ottawa (Ontario) K1A 0E6
Téléphone : (613) 991-1021
Télécopieur : (613) 990-5113
Courriel : ssopss@dfo-mpo.gc.ca

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